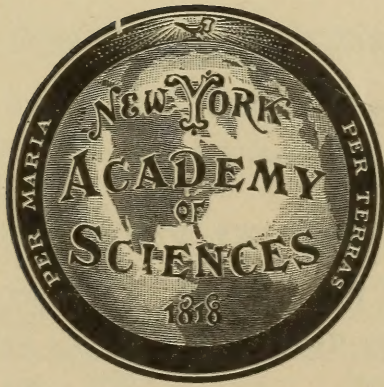


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EDMUND OTIS HOVEY



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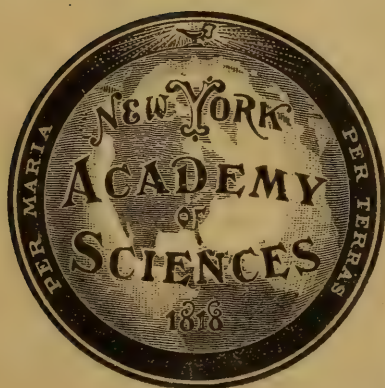
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Editor, EDMUND OTIS HOVEY

GEOLOGICAL RECONNOISSANCE OF
PORTO RICO

BY

CHARLES P. BERKEY



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The sessions of the Academy are held on Monday evenings at 8:15 o'clock from October to May, inclusive, at the American Museum of Natural History, 77th Street and Central Park, West.

GEOLOGICAL RECONNOISSANCE OF PORTO RICO ¹

BY CHARLES P. BERKEY

(Presented in abstract before the Academy, 7 December, 1914)

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¹ Based on the observations and studies of an expedition organized under the joint support of the New York Academy of Sciences and the Insular Government of Porto Rico.
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INTRODUCTION

The Island of Porto Rico has never had a thorough or detailed geological study. There have been, however, a number of papers written that have described special features or general conditions in a very ac-

ceptable manner. Most of the writings² of this kind are widely scattered in volumes of periodicals or proceedings of learned societies or pamphlets which in most cases are not readily obtained or consulted.

From a perusal of these articles, one learns that Porto Rico belongs structurally and genetically to the mountain chain now represented by the isolated islands forming the principal West Indian group. Enough work has been done, especially by R. T. Hill,³ to outline roughly the geological history of the Island of Porto Rico and indicate on a map the distribution of some of the formations. An especially good general description of physical features, also, is given by H. M. Wilson.⁴ An introductory general description, in large part along the same lines as these, will probably serve the present purpose.

GENERAL DESCRIPTION.

The Island of Porto Rico is situated in the Torrid Zone between latitude $17^{\circ} 54''$ and $18^{\circ} 30''$ north and longitude $65^{\circ} 13''$ and $67^{\circ} 15''$ west. It is the easternmost and southernmost of the Greater Antilles. It lies within the trade-wind belt, and the constancy of these winds gives the island a remarkably mild and uniform climate. There is an abundance of rainfall on the windward side, which in this case is the east end and the north side as far west as Camuy. The effect of the mountains across which these winds blow is to make the south side of the island and most of the western portion comparatively arid. Some districts are said to have no rainfall for a whole year at a stretch.

The Atlantic Ocean lies to the north and east, the Caribbean Sea lies to the south, while Mona Channel on the west separates the Island of Porto Rico from Hayti. Brownson Deep, reaching the profound depth of twenty-four thousand feet below sea level, one of the deepest spots known, lies immediately to the north. Tanner Deep lies to the south, reaching a depth of fifteen thousand feet. Although the relief of the island above sea level is less than four thousand feet, this represents only the extreme top of a great mountain mass which rises above the submerged platform, from which its real height should be measured. The extreme relief difference represented by the summit of El Yunque on the one hand and Brown-

² The writings referred to, together with others that have some description of physical conditions in Porto Rico, are listed at the end of this paper. Those of most usefulness in the present investigation are certain papers by R. T. Hill and H. M. Wilson, besides a very few others of less extended character.

³ R. T. HILL: "Porto Rico." *National Geographic Magazine*, volume 10, pages 93 to 112 (1889).

⁴ H. M. WILSON: "Water Resources of Porto Rico." *Water Supply Paper No. 39*, U. S. Geological Survey.

son Deep on the other is approximately twenty-eight thousand feet. Regarded in this way, the Island of Porto Rico belongs to one of the higher relief features of the earth.

It is in reality a badly eroded summit of a great mountain belonging to an east-west chain or range including the Greater Antilles. The general structural features of the islands are consistent with this east-west axial trend which is expressed in the topography of the central Cordillera extending from the west end near Rincon, where it starts abruptly from the water's edge, to Fajardo, where it terminates in El Yunque, the highest point on the island. The mountain range, however, is not so simple as this statement would lead one to believe, for there are in reality two ranges or branches toward the east, one of which is known as the Sierra de Luquillo, culminating in El Yunque, and the other, which is best developed in the divide between Cayey and Guayama, is called the Sierra de Cayey. The military road crosses this latter branch near Aibonito over a pass that reaches above 2,000 feet. To the westward, the double character of the mountain ranges is not so pronounced, but there is a semblance of it in the spurs that reach the sea rather abruptly, one near Rincon and the other near Mayaguez. The exact elevations of the higher mountains have not been accurately determined, the values given on the older maps being evidently too great. The revised approximate elevations are: for El Yunque, at the eastern end of the island, 3,750 feet; for El Guilarte, which stands to the west of the Arecibo road, 3,610 feet. The highest point in the Sierra de Cayey is about 3,000 feet. Many points are nearly as high as those given, and all of the roads that cross the island reach elevations on the divide that are in excess of 2,000 feet. Many of the roadways in the interior districts reach elevations over 2,225 feet.

Although the island as a whole has a mountainous aspect, and although much of the interior is very rugged and picturesque, there is usually a comparatively gentle or smooth topography along the coast, and some of the marginal areas are almost perfectly flat. These are uniformly at the mouths of the larger rivers and represent river alluvium or delta-like deposits,—they are known in the island as *playas*.

The aspect of the island as a whole is moderately rugged. Although the major portion of the rock makeup is igneous, and although there is considerable complexity of structure represented in all parts of the range, all of the surface forms are of erosional origin. The relief is that of early maturity in the interior and perhaps late maturity in portions of the coastal districts. Exceedingly steep slopes are the rule in all parts of the island where there is any considerable relief, and one of the most surprising things is the way the soil clings to these slopes. One often



C A R I B B E A N S E A

PLATE I.—RELIEF MAP OF PORTO RICO

Reproduced by permission from Bulletin 25 of the Forestry Division, U. S. Department of Agriculture.

sees slopes of this kind with angles of thirty to forty degrees from the horizontal under cultivation.

The islands of Culebra and Vieques lie to the east of Porto Rico and are said to be similar in structure and makeup, but neither of them was visited on this expedition.

The streams of the island are numerous and surprisingly large for the size of the areas drained. According to Mr. Wilson's description⁵ of the water supply there are twelve large streams flowing north, four flowing west, seventeen flowing south and six flowing east. Besides these there are said to be 1,300 small streams, and on account of the heavy rainfall on portions of the island many of them are of larger size than such an area would usually afford. The main divide runs near the southerly margin of the island, so that about one-third of the drainage is tributary to the Caribbean Sea on the south, and about two-thirds to the Atlantic Ocean on the north. This unsymmetrical position of the dividing range is an abnormal feature, the cause of which is the subject of discussion in another portion of the report. Because of the prevailing trade winds, the rainfall is very unevenly distributed. The east end and the north side are comparatively humid and plentifully watered; in contrast, the west end and especially the south side are comparatively arid. In order to overcome partly the shortage of water, a large system of irrigation is now being developed on the south side of the island. At the east end, northeast of El Yunque, there is an annual rainfall of 123 inches. On the other hand, at Cabo Rojo, at the other extreme on the southwest side of the island, it is exceedingly dry, and in occasional years there is said to be not a single drop of rainfall. Other parts of the island vary between these extremes. The wettest months are September and November.

In most districts, the underlying rock is compact enough to discourage much deep water circulation and the stream run-off is correspondingly responsive to the rainfall. In the northwest corner of the island, on the broad limestone belt extending from Aguadilla to Camuy, there is a prevailing tendency for the surface waters to sink into underground channels, leaving the surface very much more poorly watered than even the somewhat scanty rainfall would lead one to expect. In some cases, streams developed on the more compact rocks of the interior districts completely lose themselves in underground channels upon entering the limestone belt, and in some cases do not again come to the surface for several miles. Elaborate caves and channel-like caverns are common and, in the northern belt of limestone country, there are thousands of such occurrences

⁵ H. M. WILSON: "Porto Rico; its Topography and Aspects." *Jour. Am. Geog. Soc.*, Vol. 32, p. 220. 1900.

still preserved that are now wholly abandoned by the waters that formerly occupied and helped to form them. There are no inland lakes, but there are a few coastal lakes and they appear to be related to the development of alluvial plains or playas and recent elevation and subsidence changes.

The climate is strictly tropical, but it is so tempered by reason of the constant trade wind breezes from the ocean and the elevated character of much of the ground that it is usually agreeable and mild. The lack of great changes of temperature and the prevailingly moist conditions on most of the island have direct influence on the character of the rock decay and disintegration and also on the quality of the soil produced as well as its behavior as a residuary product. Other matters of climatic conditions have little or no bearing on geological problems and may well be avoided. The average daily temperature is eighty degrees; it rarely goes above ninety degrees or below seventy. The maximum temperature is ninety-nine degrees. Extremes recorded for the year indicate a range of forty degrees.

The area of Porto Rico is given as 3,670 square miles, which is about three-fourths the size of the State of Connecticut. It is roughly rectangular in outline and in actual dimensions is about thirty-five miles in average width, and one hundred and five miles long from east to west. It is the fourth in size of the West India Islands and is one of the most productive and densely populated districts in America.

Because of the greater interest recently taken in studying the natural resources and natural history of Porto Rico, it was judged to be a suitable time to make a more elaborate and detailed study of the island's geological framework and history. In accord with this view the New York Academy of Sciences organized an expedition which spent a part of the summer of 1914 on the island. The accompanying descriptions are based on the work accomplished by this expedition.

NEW YORK ACADEMY OF SCIENCES EXPEDITION

The geologists sent to make a preliminary study or reconnoissance of the Island of Porto Rico left New York on the 15th of August, 1914. Four weeks were spent in Porto Rico, the expedition returning to New York City on the 21st of September. The party consisted of Dr. Charles P. Berkey of Columbia University, New York, and Dr. Clarence N. Fenner of the Geophysical Laboratory, Washington. Arrangements were made with the bureau of transportation of the Insular government in San Juan for conveyances, so that as much ground as possible could be seen in the time available. More than 2,000 kilometers were covered by

the aid of this transportation service and observations were made in sufficient detail to judge the general character and structural relations of the formations crossed. In addition to this kind of travel on the roads, short trips were made on foot to examine features or outcrops of rock which appeared to deserve investigation, and an occasional more extended trip on horseback was taken to points in the interior. With these facilities for travel, it was possible for both members of the party to give undivided attention to geological observations. It was possible to stop and make



FIG. 1.—*Relief features characteristic of the interior ranges of Porto Rico*

Photograph taken from the Ponce-Penuelas road at K-10, looking northward across eroded formations of the older series to the main drainage divide.

brief examinations along all the roads at hundreds of places, and, on several of the roads crossing the island, sufficiently elaborate data were secured to furnish a basis for geological cross-sections showing both relief and structural features. A complete circuit of the island was made and in addition it was crossed from north to south on three principal roads. This, together with numerous side trips into the interior, permitted observations to be made on practically every formation of any considerable consequence in the island. No point in the whole area is situated more than seven miles from some road or other point of observation covered by the party, and, even in those cases, except in the extreme southwest

corner of the island, observations were made on all sides or completely around the unexplored areas. Because of the extent of the reconnoissance, it is the opinion of the writer that all of the essential, large, fundamental geological formational units have been found and their general structural relations have been determined.

OBJECT OF THE EXPEDITION

The purpose of this expedition was, first of all, to determine the nature and origin of the rock formations of Porto Rico, and to group them into series suitable for use in subsequent geological work. In the second place, it was the object of the party to determine as many of the larger structural relations as could be seen and to unravel as much of the geologic history as such a hasty examination would warrant. In the third place, the physiographic features were studied for the purpose of determining their origin and relation to the formational structure and their bearing on the more recent history of the island. Lastly, it was appreciated that the island was complex enough to have many problems that could not be solved without very much more extended investigation, and it was the purpose of this expedition to point out the problems that should receive special study and that seemed to give promise of important results. Considerable attention has been given to the economic resources of the island by private individuals and considerable money has been spent on various enterprises connected with their development. These problems were also kept in mind, and wherever convenient, special observations were made on them. Although it is possible to make suggestions concerning these economic resources, they are for the most part matters that should receive very much more extended special study. A matter that concerns the welfare of the island more directly than any of these is the question of quality and variety and origin of the native soils. These of course are in large part geologic matters also, and although this reconnoissance is not sufficiently detailed to form the basis of a discussion of this matter, it is one of the lines of investigation connected with further work that will have direct value.

INVESTIGATIONS AND DISCUSSION

ROCK FORMATIONS

The most fundamental thing to be determined at the outset of an investigation of this kind is to discover and differentiate the different rock types and the structural units to which they belong. All of the prelimi-

nary work of this expedition was devoted primarily to this question and collections were made for comparison throughout the island. In the beginning, observations were made chiefly along the coastal margins because of the greater amount of ground that could be covered and because of the apparent simplicity of the outermost and younger or more recent formations. The chief formations with their representative rock variety will be discussed in order from the younger to the older series.

In the first place, such a reconnoissance shows that there are two great series of formations separated by a marked unconformity. Both are somewhat complex, but in that respect the older series is very much more complex, both in range of composition and number of units involved and in variety of structural relation, than the younger one. In spite of this discrepancy, it is still the most convenient and useful division to make, and, because of the strikingly different characteristics of the two series and the great prominence of the structural break between them, there is no possible chance for mistaking this fundamental feature.

The whole lot of formational units are therefore grouped under the following two heads:

1) Younger Series.

Including the Tertiary shales, reef limestones and recent deposits.

2) Older Series.

Including a complex group of formational units,—tuffs, ashes, shales, conglomerates, limestones and a great variety of intrusives, all of which are probably of pre-Tertiary age.

There are several possible subdivisions of the younger series, but in this discussion only those exhibiting enough physical constancy and character to be useful in field correlation are taken into account. These are especially (1) the San Juan Formation, a Pleistocene sand-dune deposit, and (2) the Arecibo Formation, a series of reef limestones and associated shales and marls. Besides these, there are more local developments that deserve special discussion, such as the San Sebastian shales, the Juana Diaz marls and sandy shales, and the Ponce chalk beds; but in a broad grouping these are all phases of the larger Arecibo Formation and it will take detailed paleontologic study to make the proper subdivisions.

The older series has many formational members and their general relations are reasonably well understood, but a systematic subdivision is not yet attempted. Correlation in this series is still more difficult than in the other, because of the great variation in character laterally and the influence of igneous activities that prevailed throughout its whole development. Some of the most characteristic of these types will be described.

Younger Series

San Juan Formation.—On approaching the island by the usual route entering San Juan harbor, the first rock whose structural detail can be seen is that on which the city of San Juan itself is built. One can see that the formation is made up of strongly bedded material that has all of the structural characteristics of a cross-bedded sandstone and is resistant enough so that it forms, at this point, a promontory extending far beyond the supporting mainland and presenting a cliff face of at least 75 feet in height. A closer inspection supports all of these observations as to structure and adds the important observation that the granular material



FIG. 2.—Partially destroyed dune sand deposits of the San Juan formation

These deposits are a short distance west of Arecibo and are nearly covered with fresh dune sands of the same material.

is, in large part, calcareous in composition and organic in primary origin. The same type of material, with all of its characteristic structures, was seen at several other points along the north coast. Special studies were also made on sea cliffs of this formation in the vicinity of Arecibo, where the exposures were so well developed that good photographs of the structure could be taken. One of these is reproduced as an illustration of the characteristics of this formation. It shows exceedingly steep cross-bedding structure that measures up to thirty-three degrees dip, and there are also occasional structural lines that are almost horizontal. The rock is exceedingly porous, the grains are unusually uniform in size, and the

binding material is calcareous, attaching one grain to another merely at the point of contact. The extension of ledges of this kind of rock far beyond the possible reach of swift-flowing streams, together with the fact that the distribution is limited to certain sections of the north coast, and, in addition, the evidence furnished by the internal structure of the rock itself, lead to the conclusion that the formation is essentially an old dune-sand deposit. Sand dunes are developed on the present coast line from very similar material, but none of the very recent dunes are solidified. On the other hand, the San Juan formation seems to have been developed before certain of the later elevations and subsidences that affected the island in its recent history, so that its material is fairly well cemented and its base extends below the present water level. Its outcrops also extend to greater elevation above sea level than any of the modern dunes. It is judged, therefore, that this particular formation is the most recent of all in the island to act as a ledge former, and it is judged by its situation and content to be of Pleistocene age. See additional description under heading "Structural Features."

This is the most unusual formation in the island. It is a type seldom seen or seldom recognized, and it is one of the smallest in Porto Rico, in spite of the fact that it makes such an important showing at San Juan harbor.

Because of the prominence of the formation in the city of San Juan it is suggested by the writer that the name *San Juan formation* be used for it and that this name be confined to the Pleistocene beds representing solidified sand-dune deposits.

Arecibo Formation.—Next below and older than the San Juan formation is a great series of reef limestones and shell limestones preceded by shales that form a belt of considerable width along the north coast and a portion of the south coast of the island. In a large way this series forms a structural unit. Above it in all cases lie the recent alluvial deposits and the San Juan formation and below it lie the older and more complicated igneous and sedimentary rocks. The break between these two represents the chief unconformity in the whole geological column. The heaviest development of this formation is along the north coast between Tao Alto and Aguidilla. In this belt, the massive limestones of the Arecibo formation attain the greatest thickness observed anywhere on the island, but no opportunity was found for determining the amount accurately. There is in sight, however, certainly as much as 500 or 600 feet in the bluffs along the Arecibo River. In this belt also, especially farther toward the west, in the vicinity of Lares and San Sebastian, there are underlying shales of considerable thickness which in places carry lignitic

material and which have been the object of some exploratory work for coal. It is evident, from observations made, that the shale beds of the Arecibo formation vary greatly and in some places are entirely wanting. At the Arecibo River, for example, where the beds of the formation can be seen well exposed in the river bluffs, there is no shale development at all. The limestones lie abruptly on the eroded and somewhat weathered surface of the older formations which at this point are represented by coarse and obscurely bedded or even massive volcanic tuffs. At the best place seen, which was on the east side of the river about opposite K-66 on the Arecibo road, there were a few feet of transition material between the limestone beds proper and the unmodified tuff. It had not the structural appearance and makeup of the shale as seen at other points, however, and this part of the formation is regarded as entirely absent on the Arecibo River. Shaly beds, however, are seen again on the south side of the island and their best development is in the vicinity of Juana Diaz, where some of the beds are distinctly sandy and rather fossiliferous and carry petrified wood. Lignite is also reported from this vicinity, but no material of that kind was found by the writer. It is more than likely that the shale beds on opposite sides of the island do not correspond in horizon at all, but that structurally they are both basal beds.

The most striking development of the shale beds and overlying marls and softer layers of thin-bedded character, instead of the massive reef structure, is on the Jacaguas River south of Juana Diaz. The dips also of the formation in this particular locality are much greater than those observed at any other point. For considerable distances an average dip of 30 to 36 degrees was estimated and the total thickness represented, based upon the width of the belt, must be at least 3,000 feet. At no other point on the south side, however, was there an opportunity to see whether the beds of this character are constant or of large lateral extent. As one goes eastward, a comparatively short distance, they are almost entirely lacking. On the Descalabrado River, which is only ten kilometers to the east, the underlying older series of tuffs and intruded shales and limestones were followed to a distance of two miles south of the military road, whereas at Juana Diaz the basal shales of the Arecibo formation begin a half mile above the military road. It appears, therefore, that the formational margin is swinging rapidly southward, and it is judged, from other observations made, that there is almost nothing of it represented at a distance of twenty kilometers to the east, or, in other words, that the formation does not extend farther east than the vicinity of Salinas. At one other point on the south margin of the island, there is an unusually good opportunity to follow the successions of formations, and

that is in the vicinity of Guanica. Limestones belonging to the older series occur immediately south of Yauco and are very strongly developed there. The hills in which these beds outcrop extend southward almost continuously to Guanica, but at that point observations showed that the formation had changed and is actually part of the reef limestone of the Arecibo formation, although it is possible that the large fault observed west of Ponce may pass through this area and obscure the other structural relations. It looks, from the rapid survey, as though it would be favorable for some of these additional studies of the character of the lower beds of the Arecibo formation. Between Guanica and Juana Diaz, wherever the inner margin of the Arecibo formation was seen, it was bounded by a fault which brings the upper beds abruptly against the older tuffs and shales of the pre-Tertiary.

The formation furnishes an abundance of fossils. The lower portion or the lower beds on the south side of the island, as seen at Juana Diaz, seem to be the most promising for a determination of the age of the beds of the formation. Higher beds, forming a chalky white limestone to the west of Ponce, are also very fossiliferous, but in this area they are separated from the older rock series by a fault, so that it is quite impossible to tell how far above the base of the formation these beds may lie. It is judged that the portion of the formation seen at Guanica is a still higher horizon, but the exact age values have not been worked out. The total thickness of the whole Tertiary series on the south side of the island is very great. It was estimated that the shales and marls and limestones in the vicinity of Juana Diaz must certainly amount to three or four thousand feet. For a long distance along the Jacaguas River south of Juana Diaz, the beds stand with a dip of approximately thirty-five degrees toward the south and throughout the greater portion the character is notably different from the beds occurring farther to the west which are judged to overly them.

To the east of San Juan, along the north coast, there is much less prominence of the Arecibo formation and after passing Rio Piedras it in no place crosses the main road. There are occasional hills somewhat similar to those characteristic of the landscape of Bayamon and vicinity, but they do not reach to so great a height and are separated by very much larger stretches of low ground. The strongest development of this formation seen to the east of San Juan is that along the Grande de Loiza River between the railway and the coast. In going still farther east to the vicinity of Luquillo, the inner margin of the formation passes out to sea and the older formation reaches the shore. From this point around the whole eastern end of the island no more outcrops of the Arecibo for-

mation were seen, and this is true also of the southerly side coming from the east end through Naguabo and Yabucoa and Guayama, and still farther west to some undetermined point between Guayama and Santa Isabel. There may be, however, occurrences of this formation underlying the alluvial material along the coast at points considerably nearer Guayama than the outcrop map indicates.

The formation as a whole is essentially a structural unit. Although it is quite easy to distinguish the underlying shale member, especially well developed between San Sebastian and Lares, and although there are other structural changes, there is nowhere any appearance of unconformity or marked break in the succession. Besides, the shale member is not everywhere developed and, as a matter of fact, is seldom seen in tracing the formational boundaries. In some places, it is definitely shown to be absent, so that it seems unwarranted to represent this member as an important part of the formation, so far as areal distribution is concerned. Judging from field observations already made, the shale and marl beds are more extensively developed on the south side than elsewhere. But this is based on observations in one particular area and the member cannot be traced very far in either direction because of other difficulties. The beds lying above the shales and representing the part referred to as a more massive limestone portion are probably susceptible to considerable differentiation on the basis of fossil content, and it is entirely possible that a rather complete range of Tertiary horizons may be determined after complete paleontologic study. In the field, however, and on the basis of structural factors, there is no apparent ground for subdivision. In this discussion, therefore, the whole series of beds, from the unconformity at the base to the alluvium and San Juan formation overlying it, is referred to as a single formation and, on account of its extensive development in the region about Arecibo, it is suggested that a suitable name would be the *Arecibo formation*.

Some parts of the formation show the peculiarities and content of a coral reef, and these portions have the most irregular and most massive structures. Other parts show bedding structure more or less perfectly developed, and throughout the whole formation here and there, at irregular intervals, and usually of only very limited extent, there are more shaly facies. It is the opinion of the writer that this irregular distribution of shaly beds is responsible for one of the peculiar topographic features developed in the belt underlain by the Arecibo formation. This is the occurrence of almost perfectly flat soil-covered areas of no very great lateral extent at different levels, above which the numerous small knobs or hillocks of limestone rise, giving the peculiar haystack-like topography.

This type of topography is represented by the small level tract surrounded or dotted over with small hills, called "pepino hills" locally, standing like haystacks above the plain at many different elevations above the sea. This leads to the belief that the fundamental control in its development is the presence of a shaly bed in the series, which forms at each point the basis of the local plain. The hillocks standing above it or surrounding it represent remnants of the more massive and probably more porous and more easily destroyed limestone which has been attacked and largely removed by weathering, and especially by solution, down to the more



FIG. 3.—*Unconformity below the Arecibo formation*

This view shows the older tilted and eroded tuffs and shales below, as seen on the Arecibo River. The contact is immediately beneath the horizontally bedded limestones at about the center of the view where the chief weathering is noted.

resistant shaly soil-forming member. If this is the principal cause of the peculiar topographic form just described, it is quite easy to see that the distribution of such features should be expected to be rather irregular both in lateral extent and in actual elevation above sea level or in relation to the different horizons in the formation itself. In regarding this as the principal factor, there is no tendency to overlook the fact that the island has stood at different elevations with respect to sea level in former times, and that a corresponding difference in ground water levels would be felt throughout the border region. But there is no evidence whatever

that the numerous different levels represented by many of the small plains referred to above were necessarily connected with any of these subsidence changes. Additional comment on the hillock topography, so strongly developed in some parts of the area, is made in connection with discussion of drainage in another part of this paper.

The Arecibo formation is of Tertiary age. So far as identifications of the fossils have gone, they appear to confirm the opinion that the larger part of the formation belongs to the Oligocene epoch. These determinations were based largely on collections made in the heavy limestone beds and reefs in the vicinity of the Quelbradillas River. The shale beds lying at the base of the series, and exposed farther to the south in the vicinity of Lares, are certainly somewhat older and probably belong to the Eocene epoch. There are higher beds developed rather irregularly that doubtless represent still later time, referred by Hill to the Miocene epoch, but these determinations must be left to future detailed study of the formation as a whole.

It is considered eminently fitting to refer to some of the chief variations which have especially strong development in certain localities, by special locality designations, such as,—San Sebastian shales, Ponce chalky limestones and marls, Juana Diaz shales and marls, Guanica coral reefs, Quebradillas reef limestones, etc.

The correlating of all these and other local representatives of the Arecibo formation is a work that can be done only by extensive and detailed stratigraphic study and paleontologic comparison. This is one of the larger pure-science problems awaiting future investigation.

Older Series

Below the Arecibo formation and forming the surface in the interior, beyond the Arecibo margin, the island is made up of an exceedingly complex series of many different kinds of rocks. They include chiefly varieties of igneous rocks, both extrusive and intrusive, both fragmental and massive, ranging from small stringers or dikes or flows to large boss-like masses that cover many square miles in area. In addition to the igneous rocks of these types, there are numerous shale beds and conglomerates of rather massive habit aggregating a very great thickness, and with them are associated limestones and foraminiferal beds of considerable variety. A study of the rocks of this series for the purpose of determining their character and origin indicates that practically everything in the older series except the limy portions of the shales or the limestones proper are more or less directly of igneous origin. The coarser materials and those least affected by any secondary processes are the tuffs which are of direct

volcanic origin and are exceedingly abundant and extensive. They are found at intervals in all parts of the series, and it is impossible to say that they are either more or less abundant in those portions which appear to be older, rather than in those which appear to be younger or higher in the series. The closest associate of these materials is the bedded tuff, made up of volcanic fragments which have been somewhat assorted by surface agencies so that they exhibit some sedimentary structural characteristics. These are also exceedingly abundant and widely distributed and they pass by insensible gradations of finer and finer materials into those



FIG. 4.—*Typical shale occurrence*

This is seen along the road between Ponce and Penuelas at K-10. The beds at this point lie in a less disturbed attitude than is usual in members of the older series.

that are recognized as true ash beds. Most of these have become so thoroughly cemented, or so much modified by secondary attack, that they now present a perfectly sound and compact appearance. In thin section, however, it is easy to see that the material is wholly volcanic and that the bedding is the only secondary modification except that having to do with the binding, induration or alteration of the rock. The ash beds are probably close relatives of the so-called shales.

Shales.—Rocks of this type are developed characteristically at Fajardo, at Mayaguez near Baranquitas and at numerous other points, espe-

cially along the divides toward the west. At the two points first mentioned, in particular, they are light yellowish or reddish in color, rather porous in structure, strongly bedded and have a prominent blocky fracture habit. The exact character of these rocks is a question under study at the present time, but enough has been done to show that, in their present condition, they have been oxidized to the yellow or red color, and have been leached so that they have a porous structure and light weight due to the removal of at least a part of some constituent that is more readily soluble than the rest of the rock. Microscopic comparison with beds of the same structural relation, but of very dark color and very dense habit, leads to the opinion that the two types are not essentially different in origin, but that the lighter colored and lighter weight shales, such as are found at Fajardo and at Mayaguez, are simply the weathered equivalents of darker ones. It appears from this comparison that the shales are normally highly calcareous and that the lime content is supplied by the presence of a very large amount of organic matter in the form of foraminifera. In some cases this organic matter makes up fully one half of the rock and in all cases weathering produces a very porous effect that should be expected to be identical with the red and yellow shales occurring typically at Fajardo and Mayaguez. The siliceous content of all of the shales examined proves to be exceedingly fine and wholly lacking in granular or quartzose material such as characterizes most sedimentary shales. It is the judgment of the writer that this material in the shales of Porto Rico, instead of being the ordinary disintegration products derived from the weathering of ordinary land masses, is in reality largely ashy material of volcanic origin. With this conception of them, it would appear that even the limy shales are therefore close relatives of the ash beds, and it is entirely possible that they do not represent any great difference in history, but rather somewhat different surroundings during accumulation.

Limestones.—Besides the shales, there are massive limestone beds of several different types.

In most cases the occurrences are separated by structural complexities that make it uncertain about field correlation, but undoubtedly later field study will connect some of these and additional paleontologic study will arrange their succession. The most prominent occurrences seen are described below.

Coamo Tuff-Limestone.—The limestone with the closest genetic resemblance to the types already described is represented in a broad belt passing from south to northwest across the upper end of Coamo Reservoir near Coamo Springs, and which can be traced in prominent development

westward across the Descalabrado River to the Jacaguas Reservoir. Similar limestones are found at other points on the south side of the island and are judged to belong to the same member of the older series. Because of the strong development in the vicinity of Coamo Springs, and because of the fact that it represents a type so striking as to be recognizable as a field unit, the limestone has been called by us in the field the *Coamo Tuff-Limestone*. It is developed in the vicinity of the Coamo Reservoir to a thickness of several hundred feet and its most characteristic appearance is the brownish mottled color effect produced by the



FIG. 5.—*Interbedded coamo limestone layers with massive tuffs*

This formation is seen at the military road crossing of the Descalabrado River.

presence of fragments of tuff and accumulations of ash. In some beds this material is so abundant as to make up almost the whole rock and it becomes an interbedded tuff layer. Occasionally the limestone beds are very pure and almost entirely free from volcanic materials, and there are also numerous beds of real volcanic tuff, but typically there is an intermixture of tuff materials with the lime in great enough abundance to give a brownish spotted or mottled effect. An equally characteristic feature of the rock is its concretionary or nodular appearance due to algaous growths to which the lime accumulation is chiefly due. The finest development to be seen anywhere in the island is on the Descalabrado

River at the point where the military road crosses it. A photograph of the interbedded relation of tuff and limestone at this point accompanies this discussion. This is probably, in part at least, the rock referred to by Hill in some of his discussions as "mountain limestone." It seems to us that the several occurrences of limestone beds which have clearly different relations in the series, and the probability of being able to place them in different horizons, based on this content, makes it desirable to use more characteristic local designations for them. Such usage cannot be confusing even if it should be proven, as it may very well be, that some of them are identical. In this discussion, therefore, wherever possible, the chief occurrences that are not clearly identical with formations already described are characterized by adding the name of the locality where there is especially good development of the formation. A limestone seen at Coqui, considerably farther east, and several occurrences near Yanco, and others still farther toward the west, have many points of resemblance to the Coamo limestone. In some cases even the brown volcanic spots are also present, but this is not true of all places. The most constant index as seen in the field is a fine meshed coralline fossil form, strikingly resembling a piece of loosely woven cloth.

The limestone beds developed at Coamo reservoir, however, rarely show this type, but instead have a remarkable development of algæ of the form known as *Lithothamnium*.

Trujillo Alto Limestone.—There are several other limestone members in the older series. One has been observed only on the north side of the island in the vicinity north of Trujillo Alto and in the vicinity of Loiza. This is a very dense fine bluish limestone made up wholly of fine microscopic organic growths. In some places it has a rough fragmental structure, but for the most part the rock is massive and the abundant organic content, largely algæ, is its most striking characteristic. Whether it is younger or older than the Coamo limestone has not been determined, but that it belongs essentially to the same general series is quite certain. On account of its distribution it is conveniently referred to as the *Trujillo Alto limestone reef*. This member probably has a very moderate thickness and no great areal distribution. It is affected by solution developing caves at the Trujillo Alto locality in much the same manner as is the Arecibo formation, but this rock is a much more compact type and its content and structural relations are quite distinct. It was probably of reef origin also, but is associated intimately with the upper shale members of the older series rather than with the Tertiary series.

"Shred" Limestone.—Another limestone may be seen at several places on the Arecibo-Ponce road on the south side of the divide from K-13 to

K-19. It has no great thickness, but there are several independent beds. Its most striking character is the presence of patches of dark color distributed in a shred-like way through the grayish mass. The rock as a whole is massive, exceedingly compact, of a bluish gray color, and, except for these dark-colored shreds, shows no recognizable structure whatever. They contain algæ, however, which are expected to determine something more definite about their position in the series, but they are obscure forms, and doubtless considerable work will have to be put on these beds to determine their exact horizon. They are intimately associated with a series of igneous fragmental beds and a considerable thickness of very red shale or ash beds. Together these alternating limestone and red fragmental beds make a striking structural succession which was not seen anywhere else. They lie in a position which is not far from the point where the Coamo limestone belt should be expected to cross the Ponce-Arecibo road, but no such structural development has been noted at any other place. It is, of course, possible that the fine red ash represents the tuffs of the regular Coamo formation and the "shred" limestone represents a phase of the Coamo not developed elsewhere, but the striking physical difference encourages the making of a distinction, at least for the present.

La Muda Limestone.—A rather heavy development of limestone in the vicinity of La Muda between Rio Piedras and Caguas has some superficial resemblance to the beds just described from the Arecibo road, but their relationship is not fully determined. The rock is not prominently tufaceous and is not marked in the same way. It has in places a coarse fragmental structure almost completely obscured by healing and it is, as usual, attacked by cave development. Some of the caves have collapsed, leaving a complex aggregate partly made up of igneous material filling the former chambers. A conglomerate bed lies below the limestone and shale at this point and both are cut off abruptly by a large intrusive mass. How these are related to other typical members of the older series is not known, but it will be possible to trace the beds to more definite relations. This is probably one of the oldest limestone members in the pre-Tertiary series. It is conveniently referred to as the *La Muda Limestone*.

In addition to this there are very numerous small or thin local developments of limestone layers distributed through the shale beds at various points. These are taken to be, in most cases, simply somewhat more heavily developed limy layers of the same origin as the rest of the foraminiferal and ashy shales; but the nature of their origin shows that it is reasonable to expect a development of calcareous content sufficient to make them more of a limestone than a shale.

"Mountain Limestone."—In some localities, such as that near Barranquitas, and probably at other points along the same divide, the shaly beds become very calcareous, as has been pointed out by Mr. Hill. These were referred to by him as limestones and are probably included in his "mountain limestone" and estimated that the thickness of such beds amounted to fully a thousand feet. The prominence of the shaly structure in these beds and their apparently close genetic relation to the type described in this discussion as shales, leads us to regard this occurrence as essentially the calcareous extreme of the shale series. As already noted, the shales are characteristically calcareous and some of them are predominantly so.

Corozal Limestone.—At Corozal, a fragmental limestone was seen just south of the village. Its relations were not worked out and its meaning is therefore not well understood, but its structural peculiarities lead to the suspicion that it may be associated with volcanic fragmental accumulation. It was found that in at least one place in another part of the island there had been volcanic outbreaks through heavy limestone beds, and it is evident that fragmental material from such activity might therefore include a good deal of simple limestone fragments. It is hardly conceivable that they would in most places accumulate in enough abundance to make a limestone bed a second time, but such a thing is doubtless possible.

Conglomerates.—There is a very extensive development of conglomerate occurring in a belt whose general trend seems to be from southeast toward the northwest, crossing the military road between Aibonito and Coamo. There must be a total thickness of strata, including shales and interbedded tuffs with occasional small limestone, of perhaps several thousand feet. In all parts of the formation where conglomerate is developed, the pebbles represent the same kinds of rocks as were encountered in the tuffs and intrusive masses. Actual representatives of previously solidified bedded material or indurated ash or shales are very rare, but in one case at least a pebble was observed that was judged to represent a fragment from an older silicified tuff. As a matter of fact, the materials are practically all of simple igneous character and the matrix in most parts of the formation is very abundant, or even predominant, the particles of which are of the same igneous material. The distribution of material and the range of composition leads one to believe that this conglomerate represents a special state or condition whereby materials of essentially tufaceous origin were, immediately after their volcanic eruption, worn, rounded, somewhat assorted and bedded and mixed with related material. At the point examined, there was no satisfactory

evidence of marked unconformity between the conglomerate above and the underlying series of formations. But the fact that the conglomerate beds, which follow to great thickness, are prevailingly of simpler structural habit, as compared with the calcareous shales, ash and tuff series immediately below, suggests that there may be a break here of larger consequence than is observed in other parts of the pre-Tertiary or older series.

The development of so extensive a series of conglomerates doubtless does represent a considerable change in physical conditions, compared to those controlling simpler deposits which preceded and followed them, and it is possible that it may be found useful in separating the complex series of older mixed bedded rocks and tuffs into an older and a younger division by using this conglomerate as a dividing member. This is supported to some extent by the occurrence of a conglomerate of similar character but of very much less extent on the north side of the island, several miles south of Bayamon, and also one of apparently less prominence near La Muda. If additional field work should show that the conglomerate belt could be traced from one side of the island to the other, it seems to me that it would be entirely practicable to make this division.

The conglomerate is invaded by igneous intrusive material in much the same manner as is observed in the other rock formations, but the massive habit of the rock as a whole leads to a predominance of transverse dike-like masses rather than the simpler looking sills. At one point in particular, however, near K-86 on the military road between Aibonito and Coamo, the conglomerate has been invaded by a magma that must have been fluid enough to penetrate the porous matrix surrounding the conglomerate pebbles where it now exhibits a crystalline habit. This injected matrix is essentially a coarse diorite porphyry in composition, through which the pebbles are distributed in the manner that they seem to have had in the original rock, so that there are still obscure traces of bedding structure. There are additional petrographic peculiarities in this rock that will be described under a different heading. This tendency of the dioritic magma to penetrate and incorporate fragmental matters was noted in several other places. It was most strikingly exhibited in certain intrusive members cutting through tuffs and shales. In some of these cases there is so great a quantity of fragmental matter as to wholly obscure the true nature of the rock unless one can see the structural relations. In the case of the conglomerate, however, the crystalline habit of the matrix is a striking feature and it is very evident that it is wholly different from the regular conglomerate habit.

Tuffs.—The most abundant of all of the rock types is represented by a great variety of volcanic tuffs. These accumulations seem to be the fundamental basis of the whole island. Whatever has been formed in the way of shales, sandy beds or conglomerates or any other of the ordinary sedimentary types seem to be directly derived from the same material that makes up the tuffs and the rocks directly associated with them, related in an interbedded succession. In most cases, the tuffs are essentially massive in their structural habit and are made up of a complex accumulation of large and small fragments of volcanic materials which prove to be chiefly andesitic and closely related porphyritic types. There is great variety in texture and minor structure and present condition, but on the whole there is enough uniformity of actual composition to justify classing them all as andesitic tuffs.

In very many places there is obscure bedding structure indicating a tendency to assort and work over this material at the time of its deposition. This is especially noticeable in the finer materials and some of these beds are made up essentially of ash. These ash beds resemble the type referred to as shales so closely, in some places, that it is impossible to distinguish between them in their field appearance. I judge also that there is practically a gradation from one rock to the other, the ash beds showing transitions to shales, especially where they have developed under conditions encouraging much weathering and working over of the fragmental materials and promoting the growth of organisms in sufficient amount to make the accumulating beds somewhat calcareous in composition.

Tuffs and ashes are well known to be especially liable to attack by alteration and to the ordinary changes that modify rocks. It so happens, therefore, that many of these representatives are completely modified and have become so dense that they exhibit none of their ashy or fragmental structure without microscopic examination. In this condition they are usually also exceedingly hard and as resistant to destruction as the hardest crystalline rock. The largest development of massive almost structureless tuffs which were seen occupy the Sierra de Cayey between Guayama and Cayey and also the range along the military road toward Aibonito; but there are extensive occurrences in many other sections. Some of the most prominently developed bedded tuffs and ash beds were seen on the north flank of El Yunque along the Sabana River and on the north side of the divide below Comerio, and also along the Ponce-Arecibo Road both near the summit of the range and farther to the north midway between Arecibo and Utuado.

From what was seen of this type of rock, it was not possible to form a

definite conclusion concerning the age represented except by their relation to certain interbedded shales and limestones. It appears that the underlying older portions of the series of tuffs and ash beds have comparatively little of such interbedded calcareous material and have everywhere been modified or altered or metamorphosed to a greater degree than beds that lie higher in the series. But beyond this there is little to judge of the actual age. As one goes higher in the series, however, there are occasional prominent limestone members with which tuffs are intimately associated or interbedded, and it may be possible, by reason of these relations, to form a more accurate estimate of the geologic age of this later portion of the series.

Volcanic Flows.—In addition to the sedimentary beds of various sorts and the related tuffs, there are at occasional places evidences of volcanic lava flows. These were seen at several places on the road between Bayamon and Barranquitas. They are amygdaloidal in present habit and represent vesicular basalt and andesites. On the whole, evidences of lava flows on a large scale are wanting. This kind of product seems to have been very much more rare than the fragmental type. A more prominent thing as a structural feature is the occurrence of very numerous intrusive bodies.

Intrusives.—The intrusive masses in Porto Rico occur in all parts of the island and in all of the formations except the Arecibo and the overlying alluvial deposits. No such evidence was seen in any part of the Tertiary of younger series; but the complex series of rocks representing the pre-Tertiary, here referred to as the older series, are cut in all sorts of ways by both large and small intrusive masses. The smaller intrusives are chiefly andesite porphyry in composition and have everywhere penetrated the shales and ash beds. The commonest occurrence is in the form of small sills or sheets conformable to the bedding structure and varying in thickness from only a few inches to many feet. These sills are so perfect in form, have so little disturbed or modified the adjacent beds, and are so similar in general composition and appearance, after weathering, to the associated sedimentary beds, that it is quite impossible to determine in all cases how much intrusive and how much original sedimentary rock is involved. The only thing noticed as a rule is the uniformity of petrographic structure that seems to be characteristic of the intrusive as compared with the associated beds. The simplest occurrences of sills of this kind, which at the same time show their igneous intrusive character, were seen near Fajardo, near Rio Piedras and in the vicinity of Comerio. But occurrences of the same kind are exceedingly numerous in nearly every district and in total amount form a very great additional thickness

to the bedded rocks, shales, ash beds, etc., with which they are associated. In some cases, these invading magmas have incorporated great quantities of fragmental matter, giving the rock in its present condition a very strikingly fragmental appearance. This habit associated with its perfectly apparent intrusive relation makes a very unusual combination in the field. In many places there are included blocks of immediately adjacent rock such as one sees in the occurrence at the quarry at Fajardo Playa, but, in extreme cases, the mass is chiefly fragmental in its make-up and one could not readily interpret its history without complete field



FIG. 6.—*Diorite porphyry sills*

These sills are intruded between layers of calcareous shales and ash beds on the road near Comerio. The streaked or banded layers are shales, the massive portions, seen best at the left side of the print, are sills. A transgressive relation can be seen between the two layers at the extreme left.

determination of its relations. Such occurrences may be seen in the vicinity of Guayama on the road about a mile east of that place, and also a short distance south of Rio Piedras.

Few of these intrusive masses show anything but a rather uniform medium grain texture and larger ones have the average appearance of a rather fine or medium grain diorite. The granular appearance, however, is probably deceptive, due to the way the rock disintegrates, for thin sections made from many typical intrusive representatives are nearly all plainly porphyritic in texture.

In addition to these intrusive masses, which are of small size or at least of not very great areal dimensions, there are in a few districts large boss-like occurrences of massive coarse-grained igneous rock. The boundaries of none of these have been traced out, but it is certain from the distribution now known that in each case the area occupied is several square miles in extent. The most prominent one of this type of intrusive mass is that seen in the southeast portion of the island, including the district about Huamacao and Yabucoa and Las Piedras and Juncos. Whether or not this is all one mass belonging to a single intrusion has not been determined. The variety of composition seen in the different samples taken at different points is consistent with the presence of more than one intrusive unit; but it is also possible and quite as likely that the variety observed is wholly due to magmatic differentiation. The southerly portion of this mass, especially that near Yabucoa, is represented by a very coarse, very quartzose and almost pegmatitic granite. Farther to the north, in the vicinity of Las Piedras and Juncos, the rock has the appearance of a syenite. Although a part of the rock does show the composition of a true syenite, by far the greater number of specimens collected on this expedition show the presence of quartz in sufficient amount to make the rock a granite. It would appear, therefore, that this occurrence in the southeast portion of the island is essentially a granite mass and that it is of unusually large size, reaching practically from the coast at Maunabo to Caguas. The distance across this mass is, therefore, not less than about 12 miles north and south. In all probability it is not of quite so great an extent east and west, but these boundaries are unknown.

One other large intrusive mass was observed in the west central part of the island, in the vicinity of Jayuya and Utuado. In general appearance and texture this rock, in the average outcrop, does not differ much from that seen at the east end of the island which is commonly referred to as syenite. In this occurrence, however, such specimens as have been examined with the aid of the microscope, show the presence of quartz in most cases in sufficient amount to make the rock of granite composition. In this case, as in that referred above, there are considerable differences of composition shown by the rocks which seem to be a part of the same mass. Specimens found, for example, near Adjuntas have the compositional characteristics of diorite, whereas a specimen taken near the margin of the boss on its northerly side, near K-53 on the road toward Arecibo, is a syenite. At certain other points near Utuado, the rock is a granite porphyry.

The best idea of the variety of composition and textural quality represented by all kinds of intrusives in the island can be gathered from an

examination of the water-washed pebbles in the stream beds that have come down the steeper mountain sides. An examination of such material shows an extremely large varietal range, and, although by all means the greater number are some variety of diorite or andesite porphyry, there are occasional more basaltic and more acid types represented.

Summary.—From this description of the variety of rock types represented by the leading field units, it may be readily seen that a subdivision into members of mapable constancy is no easy matter.

It is the opinion of the writer that, for the present work and for investigations immediately to follow, local designations or names will be of most direct usefulness, and that a correlation should be expected to be the final outcome of a series of such studies. For the present, therefore, it is judged best to use the terms Fajardo shales, Mayaguez shales, Jayuya road shales, Barranquitas shales, etc., as suitable names in these respective districts for the shale member of the older series, without any intention of suggesting their equivalence. In spite of the physical similarity in these cases, it is not at all likely that they belong to the same horizon.

Similar argument will hold for most of the other members,—the ash beds, the tuffs, the limestones and the conglomerates,—and it is recommended in these cases, also, that locality designations be used in the field investigations. Those described in this report are not necessarily all that deserve special designation, but the same rule may be applied to additional occurrences without in any way obscuring the ultimate solutions of the problem of correlation. On account, therefore, of the complexity of the structure and the limited amount of work yet done in connecting the separated occurrences into continuous field units, it is advisable to retain such terms as Coqui limestone, Coamo limestone, Corozal limestone, La Muda limestone, Trujillo Alto limestone, Cayey tuffs, etc., for the earlier descriptions and special studies.

PETROGRAPHIC RANGE

There is an exceedingly great variety of certain classes of rocks in the Island of Porto Rico. Those most prominently developed and showing the greatest variation in minor character, structure and relationship are the volcanics, especially the volcanic fragmentals. All sorts of tuffs, cinder beds, ashes, mud flows and bombs are represented in great quantity, in very wide distribution and in all stages of alteration and induration.

Observations made on thousands of occurrences of this character of materials leads to the conclusion that most of it is essentially of andesitic composition. Although there is an occasional fragment of either more basic or more acid composition, the predominant types are always of

andesitic makeup. The present condition of these rocks, representing as they do nearly all stages between fresh material and either a thoroughly weathered or considerably metamorphosed condition, is a more interesting study than their primary composition. Some of the most dense and resistant rocks in the whole island are these older metamorphosed tuffs and ashes.

Next in point of abundance is the group of crystalline igneous rocks. In this case there is somewhat greater prominence of varieties represent-

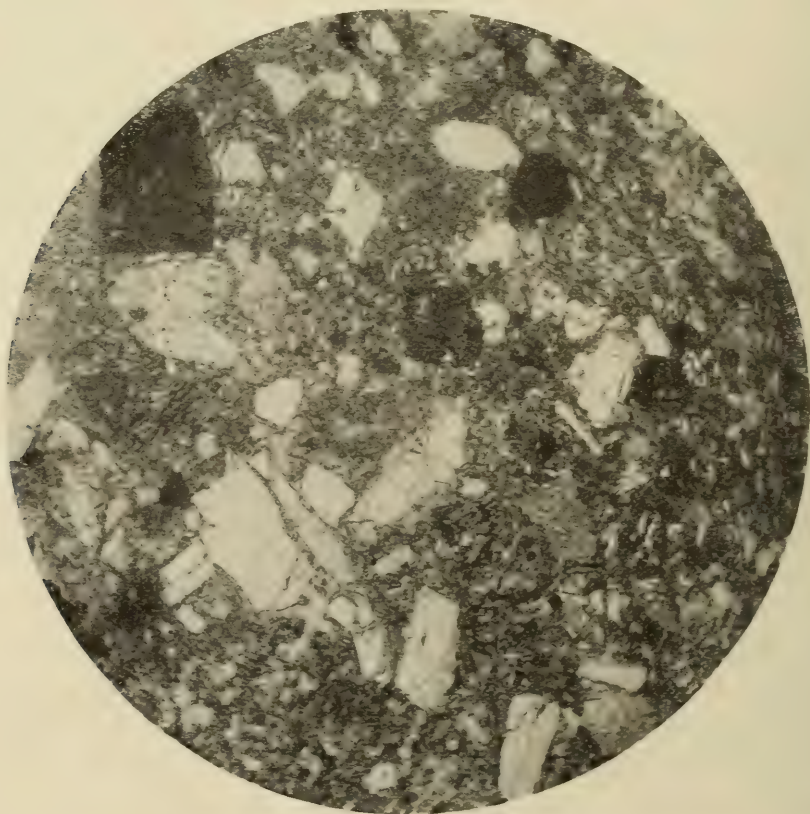


FIG. 7.—*Photomicrograph of a typical thoroughly indurated andesitic ash, magnification 28 diameters*

A rock of this type appears in the field as a dark-greenish hard resistant obscurely bedded layer, usually closely associated with more massive tuffs on the one hand or more strongly bedded shales on the other. The clear grains are mineral fragments; the more complex grains are fragments of lava, cinders, glass, etc., all thoroughly bound into a complex aggregate.

ing the acid and basic ends of the classification scheme, but here also the rocks of the andesite-diorite family are by all means the most numerous and most widely distributed. The greater number of occurrences are represented by members of this family belonging to intrusives that would be classed normally as andesite porphyries, porphyrites of various kinds and diorite porphyries. The minor variations represented by these rocks

would probably include all of the habits known to this family. In addition to the porphyries of this family composition, there are less common occurrences of felsite, quartz porphyry, granite porphyry and basalt porphyry. In surface flows there is, besides the andesites, an occasional amygdaloidal basalt, but so far as observed there was no rhyolite or other very acid surface type. Among the massive larger intrusives, the commonest and most abundant type is a granite porphyry or granite varying in some parts to the composition of syenite. A massive rock of the na-

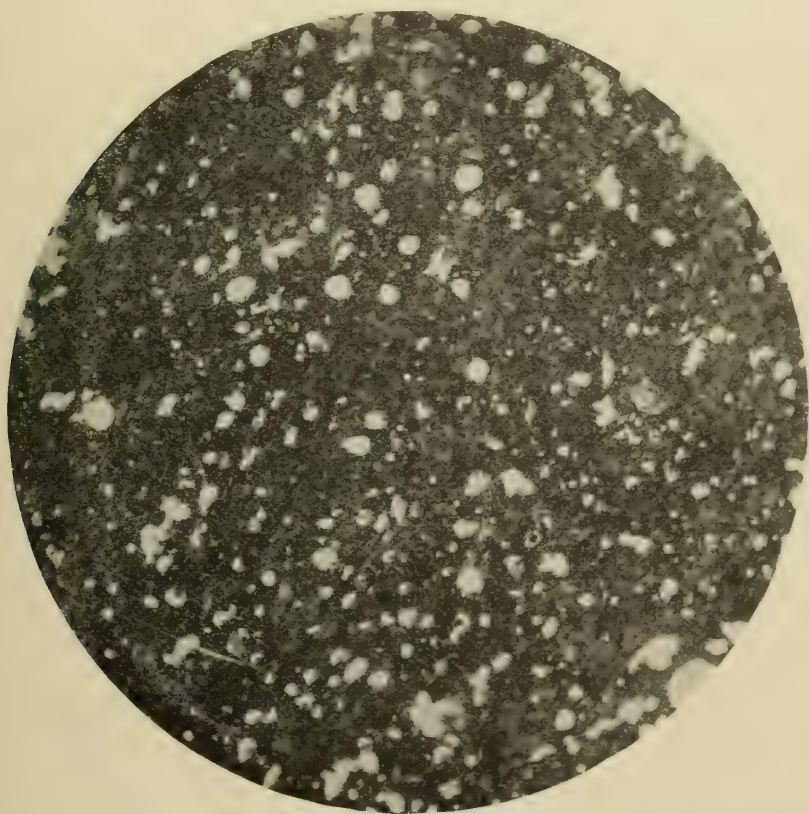


FIG. 8.—Photomicrograph of a typical weathered shale from Fajardo Playa, magnification 28 diameters

The dark field is made up of an extremely fine aggregate of earthy materials. The white circular and irregular spots are entirely empty and constitute the porosity of the rock. The circular forms of these voids suggest that they represent former calcareous content in the form of foraminifera, now completely removed by weathering.

ture of a diorite is also represented, as is a very coarse rock of the nature of a giant granite. How these are related, how many intermediate varieties there may be and whether this variation represents magmatic differentiation within a single mass or instead different units of intrusion, has not yet been determined in enough detail to make a positive statement. But in at least two cases where these large masses were seen,

the hasty examination given to them leads to the belief that differentiation effects can be traced.

The closest relatives of the igneous rocks are the sediments, and because of the fact that the material constituting these sediments has been furnished by the volcanic fragmental supply in large part, their character and makeup is in many cases not strikingly different from the ashes and finer tuffs. They do, however, represent an additional assorting, an additional weathering and an additional opportunity for intermixture of

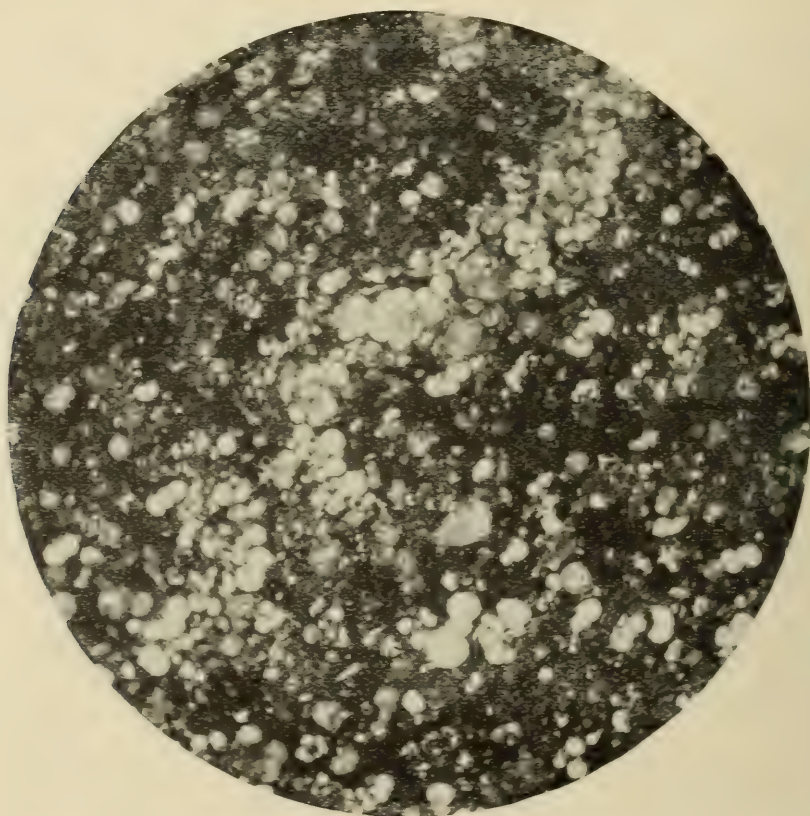


FIG. 9.—*Photomicrograph of a foraminiferal shale from the Bayamon-Comerio road, magnification 28 diameters*

The dark areas are chiefly earthy aggregates of very fine texture: the whitish areas are calcareous spots which in many cases still preserve the forms of foraminifera. It is the removal of such materials from the shales that is believed to account for their porosity as seen in weathered outcrops.

materials from different sources and of organic material developing at the same time. These conditions give a great range of composition and mineral makeup to the shales and sandstones and they merge by imperceptible gradations from simple tufaceous or arkosic sediments to calcareous rocks or even to fairly pure limestones. The common source of the calcareous element in these rocks is from an intermixture of fora-

miniferal matters representing organic growths accompanying the accumulation of the deposit.

The limestone members on the one side representing almost pure organic accumulations, and the conglomerates on the other representing the simpler destructive volcanic fragmental matters, give the range between which an exceedingly great variety of sediments are represented.

The shales of the younger series, represented by the Lares and the Juana Diaz shales, are more strictly detrital and of true erosional and

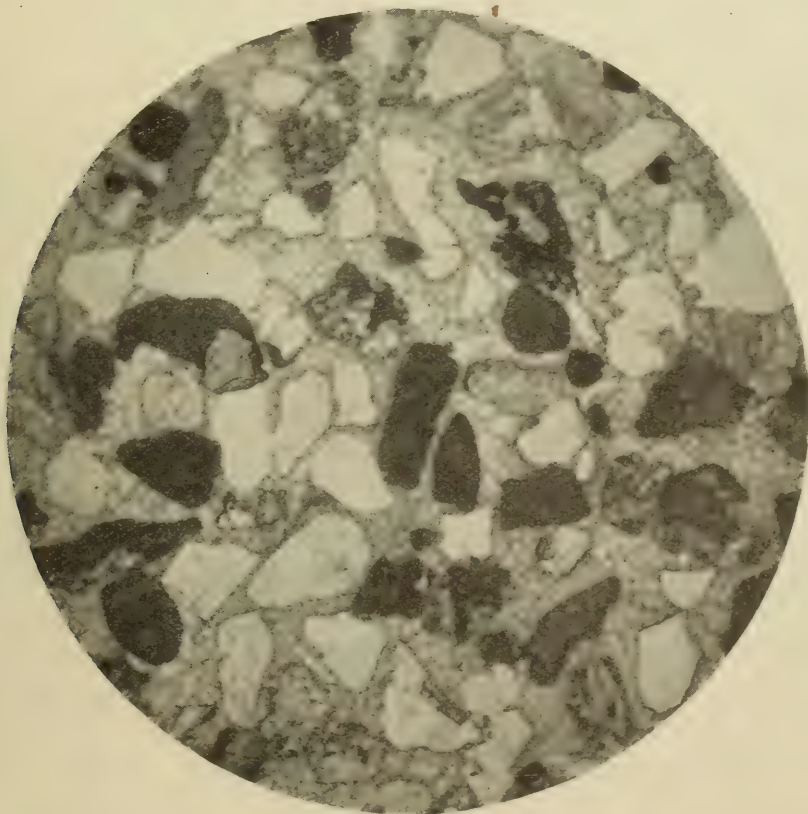


FIG. 10.—Photomicrograph of the San Juan formation indurated dune sand, magnification 28 diameters

The clearest grains are simple mineral fragments; the dark ones and the grayish ones with internal structure are fragments of calcareous organic growths. The grayish matrix is a secondary binding material of calcitic composition, in this case practically filling the interstitial spaces.

destructive origin, and in places they contain lignitic material which suggests different physical conditions. This shows, however, in their upper layers an increasing amount of organic content also, and finally are succeeded by limestones of wholly organic makeup. The failure of volcanic activity during and subsequent to that time gave no opportunity for the amount of intermixture that is seen in the shales of the older series, so that as a result the younger series of rocks is petrographically

more simple and less modified. The organic content is of greater variety, however, and because of the reef-building tendency the primary structure is more varied than is seen in the limestones and shales of the pre-Tertiary representatives.

The most striking petrographic type is, probably, the solidified dune sand making up the San Juan formation. Its uniformity of grain, strong cross-bedded character, porous habit, together with its rather surprising stability, make it an object of some considerable interest. Several of these classes of rocks, therefore, represent petrographic series of unusual range and variety, and because of their perfection of development would seem to warrant detailed study.

There are no foliated metamorphic rocks so far as yet seen in Porto Rico. One specimen of such rock, a mica schist, was shown to the writer as having come from the Portuguese river not far from Ponce, but a hurried reconnoissance in the vicinity failed to uncover anything even resembling it. The specimen probably does not belong to the rocks of Porto Rico. No evidence whatever has been seen of conditions that would be expected where such rocks occur.

The most profoundly modified rock observed is a massive serpentine. Such material was seen at two places by this party, one near Yauco and another on the road to Comerio, and the same type is reported by Professor Crampton on a much larger scale near Maricao. But they are all simple petrographic cases after all, being ordinary intrusive units of heavier ferro-magnesian content than the average which have been heavily altered, especially by hydration processes, to the present condition. Genetically and historically, the serpentines are not materially different from the other intrusive bodies.

Depth of Decay

Alteration has affected the rocks at most points to considerable depth, but in spite of this there are plenty of outcrops, and along the roads there are many cuts exposing fresh rock. The stream beds are strewn with fresh pebbles and boulders. Although decay obscures the character of the rock in most of the outcrops, the structure is usually fairly well preserved, and in most cases enough can be seen to enable one to determine the formational habit.

The most striking thing about many of these badly decayed outcrops and cuts is the remarkable way they stand against destruction or removal by ordinary weathering and erosion agents. At many points, road cuts are made, with side walls absolutely vertical, through wholly decayed rock material, that stand for years without crumbling down. Embank-

ments made of earth along roads and trails behave in the same way and one is continually surprised at the steepness of such slopes and their apparent stability. Slopes of 40° are not rare on hillsides that are cultivated, and one occasionally crosses divides that are mere knife edges with slopes of this kind on both sides. Such stability of the soil is a great factor in preserving the agricultural productivity of Porto Rico and in the distribution of its agricultural industries over so much of the interior area.

There seem to be three factors of large consequence in this stability of the soil mantle. One is the clinging character of some of the vegetation which tends to bind the soil together; another is the small range of temperature variation which reduces disintegration or disruption tendencies to a minimum; and still another is the low content of inert or refractory materials, such as quartz, in the rocks whose destruction has furnished the soils; all of which factors favor the making of especially tenacious soil. Most of the soils are for the same reason exceedingly difficult to cultivate. As a direct consequence of this soil behavior and climatic control, there is comparatively little dust formed in Porto Rico. This is especially noticeable on the roads, where one is almost never in the least troubled by it.

In two districts, one on the north fringe of El Yunque along the Sabana River and the other on the north side of the divide near Adjuntas, deposits were seen which suggest glacial action. Very large boulders are stranded in positions where it is difficult to account for them by ordinary erosion means, but too little study was given and too little evidence is at hand to warrant a more definite statement.

STRUCTURAL FEATURES

Most of the structural features represented in the geology are mentioned in connection with descriptions in other sections of this report. This is especially true of such structures as may be regarded as essentially primary, including the interbedded and intrusive forms of various kinds. There is no doubt but that the most prominent structural combination in Porto Rican geology is represented by the succession of interbedded sedimentary beds and tuffs, cut by or interleaved with intrusives in the form of sills, dikes or irregular stringers. The combination occurs in great variety as to succession, relative amounts or proportions, quality of material, present condition and relations to other members, but in spite of these variables the structural feature is essentially the same and has the same meaning everywhere.

Igneous Structures

The most striking thing in connection with the structure is the remarkable uniformity of the sills and their close resemblance on that account, after weathering, to the fragmental beds with which they are associated. The small amount of metamorphosing influence that they seem to have had, also adds to the difficulty. In some cases, however, a transgressive intrusion has disturbed the adjacent beds a great deal in a mechanical way.

In the average case, it is judged that the intruded magma has neither penetrated the materials of the adjacent beds to a noticeable amount, nor



FIG. 11.—*Shales and ash beds cut by a large irregular dike and sill*

The dike is shown at the location of the standing figure and the sill extends upward to the left between the plainly bedded layers. Both the dike and the sill are crowded with fragmental material to an extent that makes the intrusive have more the appearance of a volcanic fragmental than a true intrusive.

has it absorbed or incorporated a great deal of such material. But in a few cases where structural relations were indisputable it was equally clear that the intrusives, both transgressive and concordant, were literally choked with foreign fragmental matter, making them resemble the real tuffs so closely that it is doubtful whether the difference would have been detected except for the clearness of the intrusive relation. Such occurrences suggest that there may well be many other apparently fragmental interbeds that are in reality fragment-clogged intrusives. On ac-

count of the great abundance of the fragmental matter, it does not seem possible that these intrusive masses could penetrate in that condition to some of the positions where we now find them. It is more likely that a rather fluid magma has penetrated some unusually porous fragmental bed forming a matrix for it, perhaps also spreading it somewhat, and then in breaking across to another bed, in some cases it was still mobile enough to drag the mixture along into the larger transgressive structures. This idea is somewhat supported by the finding of a conglomerate bed, near K-86 on the military road west of Aibonito, impregnated with an igneous matrix in essentially this same manner. In addition to these forms, there are numerous larger intrusive masses, the largest of which deserve a special name. I see no objection to calling them bosses. The two largest occur, one between Caguas and the Caribbean sea toward the south and southeast, and the other between Jayuya and Utuado on the north side of the divide.

Volcanic Vent Complexes

A special igneous structure that has not been referred to except incidentally is that composite of disturbed structures which represents the location of old volcanic vents. They are essentially a complex of irregular intrusive units cutting and including masses and aggregates of various fragmental and sedimentary types in a mixed relation. In the clearest cases, such a complex suddenly takes the place of a formation of apparent promise of continuity such as a series of sedimentary beds, and after an interval these beds are again found continuing as before. For example, the Coamo limestone formation is abruptly cut off and its place is taken for a mile or more by one of these igneous complexes, the limestone continuing on the other side again. The Jacaguas reservoir, just above Juana Diaz, lies in one of these old volcanic-vent complexes, occupying, however, only a portion of the area. Another such case is represented by the complex cutting the great conglomerate beds on the military road at about K-87-88 west of Aibonito. Another is believed to be represented by the very striking basin-like area crossed by the road between San German and Hormigueros. This one is now represented by a very smooth plain five or six miles across surrounded on all sides by more hilly country. The same conditions are undoubtedly indicated by the extremely complex structures seen on the Descalabrado river two miles below, south of the military road. Some of these mark the sites of ancient craters, clogged or choked with fragmental and intruding materials.

Folding

Most of the rock formations representing original bedded types have been more or less tilted or otherwise do not now have their original attitude. Those belonging to the younger series, the Tertiary limestones and shales on the north side of the island, are comparatively little disturbed, and in some cases do not have a very different dip in spite of the fact that they have changed very much in position with respect to sea level. On the south side of the island, however, even these later beds are in many places tilted at a higher angle than they had in the beginning



FIG. 12.—Overturned fold and crush zone in finely bedded shales on the Jayuya road near the summit of the range

and occasionally show high angles and even gentle folds. This condition may be seen on the Jacaguas River, near Juana Diaz, better than at most places, but similar conditions are indicated by the relations at certain points farther west. This condition on the south side of the island indicates more extensive and more violent dynamic disturbance on this side, which is further supported by the presence of faults cutting and affecting the Tertiary series on its present inner margin.

The older series, the pre-Tertiary, is still more profoundly affected and, in almost all districts, shale and ash beds may be found standing at high angles, in many cases practically vertical, and in occasional instances

crumpled and overturned in a most complicated manner. Minor fold structures of this kind are especially prominent in the higher ranges, for example, along the Jayuya road along the divide opposite station K-24 of the Ponce-Arecibo road. At such a place may be found as complicated structural features of this kind as is usually present in any folded mountain region. The high angle at which such beds stand at many other points leads to the belief that similar complexities characterize a great many of the districts occupying the higher mountain portion of the island as well as some of the marginal areas, but the great amount of erosion and the very limited exposures at most points tend to obscure some of these details. The complex way in which the igneous intrusive masses cut all of these formations also tends to obscure and modify and further complicate the simpler fold structures so that it is not always possible to properly credit the disturbed attitude. On account also of the fact that the total quantity of injected or intruded materials, including dikes, sills and bosses, is exceedingly large and must have caused extensive disturbances by reason of the displacement produced by the occupation by these intrusive masses, it is likely that much of the observed abnormal attitude of the bedded rocks may be due to this cause rather than to regional folding of a simpler sort. It is fair to say, however, that a sufficient amount of data is not yet available to draw general conclusions as to the meaning of the fold structures in Porto Rico. The striking thing is that all of the older formations are disturbed and that their position and attitude, even along the margins of the island, indicate that the region affected by these movements was more extensive than the present land area.

Faulting

There are many evidences of faulting on a small scale, in some of which the displacements can be measured. But in most cases the direct evidence lies chiefly in the existence of crush zones, slickensided walls and abrupt changes of rock type; there is no opportunity, on account of the general rock complexity, to secure quantitative data. Judging from the difficulty in tracing certain formations between districts where they have been identified, it is probable that there are occasional faults of large displacement. Numerous crush zones were seen on the Comerio road especially, but in this case also no system was discernible from the few measurements available.

The most prominent fault, in its effect upon present features, is the one now marking the inner margin of the younger series of chalky limestones and shales constituting the coastal belt along the south side of the

island from Juana Diaz past Ponce at a short distance to the north, crossing the Ponce-Arecibo road at K-4.8, and thence westward, crossing the Ponce-Penuelas road at K-10. This is the only large fault actually observed that is necessarily of recent age, although a few others are inferred. It must be of very late Tertiary age, because the chalky Ponce beds are abruptly cut off by it. The older rocks of the pre-Tertiary are lifted with respect to the younger series forming the present coastal margin wherever this fault has been seen. It has been traced by us from Juana Diaz to the vicinity of Penelas, a distance of about 12 miles. What becomes of



FIG. 13.—*Crumpled shales as seen along the Jayuya road near the summit of the range*

it at either end is not yet determined, but it is believed to extend much farther in both directions.

The physiographic habit of the island as a whole tends to support the view that the fundamental structural form is that of a large fault block, with the principal fault displacement and uplift along or near the southerly margin, tilting the whole mass gently northward. If this disturbance took place, as seems to be indicated by the fault described, in very late Tertiary time, accompanying the emergence from the sea, it would account for the abnormalities of Tertiary rock distribution as well as the unsymmetrical position of the main drainage divide. In any case, however, the fault block structure is a very late development and is superimposed on the other more complex and older structures of the mass.

The island is comparatively abruptly terminated at both the east and west ends. The younger limestone margin, which is fairly continuous along the north coast and extends along about half of the south coast, is wholly wanting at the east end and is also absent at the west end except at the corners. At Fajardo, at the east end and at Rincon, at the west end, for example, the older complex bedded rocks continue to the shore line. In the uplifting of the present island mass, it would therefore appear that breaks occurred at both ends. The included mass is therefore probably bounded roughly on three sides by faults, the east, west and south, and is as a block tilted gently to the north.

That there is, besides, considerable differential movement accompanying the uplift and disturbance, is indicated by the warping of the erosion plain lying beneath the younger series, the Eocene peneplain, which stands essentially at sea level in the vicinity of Loiza and more than a thousand feet above it at Lares. This difference is accompanied by a much wider belt of these later limestones also in the region about Lares than elsewhere. Such warping need not of course be confined to the last movement; it may have accompanied the depression in early Tertiary time, permitting, as is indicated by deposits, very marked differences in the development and encroachment of the organic accumulations.

Large Structural Groups

Where rock formations or field units are so numerous and so closely related and so complex in primary structure if taken in detail, it is advisable to combine them into fewer more generalized groups. A first step of a very general sort, but in all respects sound, has been taken in recognizing and using the terms "Younger Series" and "Older Series" in this paper. An additional step has been suggested in recognizing certain smaller associations under the terms San Juan Formation, Arecibo Formation, Coamo Limestone Formation, Juana Diaz shales and marls, Fajardo shales, Sierra de Cayey tuffs, Ponce chalky limestone, etc., but these are for the most part local designations, some of which may well be expected to become unnecessary after complete correlation is established. A good structural basis for sound subdivision of this sort is not yet worked out.

Unconformities

There is only one marked unconformity in the structure of the island. This is between the younger and the older series. It measures the break in the sedimentary succession represented by the erosion interval during which this mountain mass, now represented by Porto Rico, was reduced

to a comparatively monotonous surface for the most part at least near to the sea level. The time interval need not have been of very great geologic value, but it represents the time between the last violent outbursts of volcanic eruptive activity, occurring near the close of the Cretaceous, and the beginning of simple sedimentation and limestone reef development and other organic accumulations in the early Tertiary. This unconformity is very pronounced along the northern margin of the island wherever the two principal series of formations are well developed. This is not easily seen on the south side, but the relative complexities of attitude of the two series, together with their position, emphasizes the same fundamental relation. This break in sedimentation is not anywhere marked by a development of a basal conglomerate. In some places the new series is inaugurated by the development of shales, part of which are lignitic, indicating land conditions, but in other places such beds are entirely wanting and the upturned eroded members of the older series are followed abruptly by limestones of the reef type. The first type of succession is illustrated in the vicinity of San Sebastian and Lares and the latter type of abrupt limestone succession by the conditions seen on the Arecibo River. It is entirely likely that the time value of this break is not everywhere the same. Probably the districts in which shale beds are developed saw the beginning of sedimentary deposition at an earlier period than those in which the shales are entirely lacking. It will be possible to work out these historical and structural differences with further study of the content and distribution.

A very extensive development of conglomerates in the region immediately west of Aibonito and smaller occurrences at several other points, especially on the Comerio road south of Bayamon and also near the military road in the vicinity of La Muda, have a suggestion of the possibility of a rather important structural break, but there is thus far no conclusive evidence of the presence of any real unconformity.

Veins

Quartz veins are not prominently developed. There are occasional quartz stringers and in a few places they are abundant enough to make a sort of net work, but in no instance was a large persistent fissure vein seen. In some cases the stringers of quartz carry values in gold, and in all probability they are the source of the placer gold known to exist in certain districts. So far as observations have been made, there is no particular system represented in the vein occurrences. Questions connected with this subject together with mineralization and possible value as mineral resources should be made a special study.

Minor Structures

Although there is extensive development of sedimentary formations which have been subjected to much disturbance, there is comparatively little structure of a minor sort that seems to deserve such discussion in this description. Two, however, that seem to have special significance connected with the origin of the particular beds which have been found are (a) a peculiar crumpled, enterolithic structure seen in one of the ash beds near Guayama, and (b) the wind-assorted cross-bedding structure of the old dune sands of the San Juan formation at Arecibo.

Enterolithic Structure.—The enterolithic structure noted in the ash beds, on account of the thinness of the bed,—about eighteen inches,—and the simplicity of the associated structure,—simple tilted beds,—leads one to believe that the structure is essentially primary rather than of subsequent dynamic origin. Its appearance is perfectly consistent with the explanation that it is preserved from the time of deposition and its behavior at that time as a small mud flow. It is a structure such as might be formed by slumping movement of a soft layer. It should be expected that there would be frequent behavior of this kind in the accumulation of such extensive beds of ashy materials, which must in some cases have been deposited under conditions that would make slumping movements possible, but it is not to be expected that material of this kind would in most cases be capable of preserving any of these primary movements. In the case noted, the quality of the interior makeup of the bed seems to have been more favorable to such preservation. It is the only case where such an observation was made.

Double Cross-bedding.—The cross-bedding structure belonging to the San Juan formation is a prominent feature wherever these ancient dune sands are preserved. A great prevalence of steeply inclined minor structures is crossed by fewer nearly horizontal ones. Measurements made on sea-cliffs a short distance west of Arecibo, where this rock is very prominently developed, gave dips of 30 to 33 degrees repeatedly. A series of these is abruptly terminated by a more nearly horizontal bedding for a comparatively short distance and the whole structure is repeated. The layers with this kind of structure are prevailing one-half to two feet thick and no ripple marks were seen on any of the beds examined. The cross-bedding structure in this case dips always to the west or southwest, and the average strike of the principal beds is about north 30 degrees west. This is consistent with a wind direction not very different from the present prevailing winds. Very strong structural development of this kind is also to be seen in the city of San Juan at the promontory on which the

Morro is built, but measurements of orientation were not taken there. An occurrence of this rock immediately to the east of Arecibo, a short distance south of the lighthouse, showed structures of this kind on a much larger scale than was seen elsewhere, and with an especially interesting combination structure. The principal or stronger divisions are widely separated and lie nearly horizontal. A comparatively small bed lying in this position was almost unconsolidated, but those strongly cross-bedded immediately above as well as those below were compact enough to stand in a vertical cliff 30 to 40 feet high. The chief interest attaches



FIG. 14.—Cliff of the San Juan formation south of the lighthouse at Arecibo

The prominent cross-bedding, extending throughout the upper thirty feet of the cliff, is well shown, together with a less strongly marked horizontal structure crossing the same beds. The prominent break near the base is made by a layer of sand which is very poorly consolidated.

to the strongly cross-bedded portion forming the upper twenty feet or more of the exposed cliff. The cross-bedding structure itself extends without interruption through a much greater vertical range than in any other outcrop examined, but its attitude and dip were not markedly different; the feature that was strikingly different from the structure seen anywhere else was introduced by the presence of less pronounced but still very plainly marked horizontal structures, making an interpenetrating mesh-like arrangement in the face of the cliff. This can be seen strongly enough to show in a photograph even at a distance of 100 feet. It is evi-

dent that some peculiar condition has been in control in the development of this compound structure. There is no reason to assume any difference of source or origin for the steeply inclined structures, or cross-bedding structure, from that assumed for all of the other occurrences of the San Juan formation. It is apparently a perfectly normal product of the assorting action and deposition of material under the work of the wind. But under normal conditions it would not happen that a second structure in a horizontal position should be repeatedly developed crossing the well marked cross-beds so that the whole complex combination should be developed on such a scale as is seen in this case. From the nature of the deposit and the conditions in which it may well be assumed to have been formed—that is, at or near sea level in the vicinity of or bordering upon standing bodies of water—one would be inclined to favor the explanation that the accumulating cross-bedded sands fell into or rolled into a body of water which had a tendency to attack the newly deposited material and to bind the grains together. The difficulty with such an explanation is in the fact that the horizontal structure is repeated at small intervals practically throughout the deposit, and apparently without disturbing the primary depositional structure at all. It would seem quite unlikely that loose matters of this kind, falling into or rolling into a body of water of an open surface sort, should maintain or preserve the primary structure so well. Perhaps it is more logical, in view of all the features, to connect the development of this structure which seems, from its slight influence or modification of the cross-bedding, to be wholly secondary with the subsidence of the coast which is shown to have been one of the late events in the geological history. As subsidence progressed, perhaps somewhat irregularly, it would happen that the ground water level would rise correspondingly high in beds that were passing below sea level. At the surface of this ground water level the tendency would be to accomplish a binding of the granular materials together. Both above and below the ground water level there would probably not be so strong a tendency to develop this binding. With the next step in the progress of subsidence, another streak or indurated zone would be established and these have been repeated throughout the whole formation during the whole period of subsidence. An action of this kind would not tend to disturb the primary structure at all; it would on the contrary tend to preserve it or make it less destructible because of the improved induration. But it could, in addition, develop a succession of secondary structures throughout the whole mass which, if the binding is fairly substantial, might rival the primary structure in prominence when exposed to subsequent destructive attack. It is possible that such a succession of horizontal struc-

tures could be developed even under a perfectly continuous but very slow subsidence movement by reason of the natural seasonal ground-water fluctuation. From this point of view, the range between two succeeding



FIG. 15.—*Detail of the double structure in the San Juan formation at Arecibo*

This photograph was taken at the same point as the one shown in Figure 14 to bring out the horizontal structure crossing the inclined layers. There is no doubt whatever that the dark layer of less consolidated sand in the lower third of the photograph is a primary bedding structure, but the horizontal marks crossing the inclined layers in the upper part of the view are believed to be of secondary origin.

horizontal markings would measure the fluctuation range of the ground water, the harder zones representing in that case the more persistent upper level for each succeeding depression position.

The cross-bedding structure shows as plainly as it does on exposed surfaces also because of the fact that certain streaks are more perfectly indurated than the intervening ones, and the objection might well be raised that a history of the kind suggested above would not be expected to develop such a difference of induration in layers inclined at such high angles to the horizontal. As a matter of fact, however, these sands are not simple in their makeup. They are in large part fragments of organic material and complete shells of small organisms of a calcareous nature and the primary cross-bedding structure represents an assorting action on this mixture of silicate and carbonate mineral material. It so happens, therefore, that the successive structural units are not necessarily of the same mineral proportions, and in the process of induration, or of binding the grains together, certain streaks yield more readily to this influence and develop greater solidity and resistance to destruction. It happens, furthermore, from a variety of rather unusual primary conditions and secondary influences that both a primary and secondary structure of unusual prominence and peculiar association are developed in the San Juan formation.

SPECIAL RELIEF FEATURES

Playas

The flat areas along the coastal margin which are known as playas are all developed at the mouths of rivers and are essentially alluvial deposits of floodplain and delta type. In most cases they seem to occupy areas that must formerly have been embayments in the coast. This development is most striking, for example, at the mouth of the Arecibo and of the La Plata and Loiza rivers. In some cases, however, there is no marked embayment and the deposit is more strictly marginal, such, for example, as the Fajardo Playa at the east end of the island and others on the south coast.

Promontories

In addition to the embayments and playas, there are, occasionally, in the intervening spaces, promontories where the rock formations extend into the sea and terminate in cliff forms. These are neither numerous nor are they confined to any particular portion of the island or to any rock formation. They are represented by the most recent of all of the

formations, essentially a silicified dune deposit such as that at San Juan, also by Tertiary limestone reefs, such as that at Quebradillas and at Guanica, or by the still older igneous and clastic series, such as that at Anasco, or by massive intrusives of a strictly igneous habit, such as that at Maunabo. It would appear from this that the former outline of the island must have been more irregular than it is at present and that the distribution of marginal formations is also not as regular as has been represented in earlier reports.



FIG. 16.—*Playa plain and marginal terrace*

View of the Playa plain (foreground), the marginal terrace (middle field) and the mountainous divide formed by the Sierra de Cayey as seen from the "Central Machete" near Guayama. This terrace bevels across the upturned edges of shales, ashes and intrusives of the older series and is probably due to marine cutting.

Terraces

At many places on both sides of the island there are comparatively smooth tracts having the appearance of bordering shelves which represent true terraces. Their location along the sea margin and the comparatively insignificant development of similar benches along the streams lead one to believe that they have an origin connected with the wave action and attack of the sea. This interpretation is supported by the presence of these terraces along the coastal margin where stream action would not seem to have been able to reach. In any case, the presence of such terraces, which stand from 100 to 200 feet above the present sea level, indicate a former more submerged condition, so that the sea or streams, or both combined, were able to attempt base-leveling at that ele-

vation. The presence of great quantities of roughly assorted gravels clogging some of the valleys of the southerly side of the island tends to support the **same** general conclusion. The bearing of these features on the geological history of Porto Rico will be taken up at another point.

Cuestas

Both on the north side, for nearly the whole length of the island, and on the south side, over the westerly half, there is a bordering belt of limestone and associated beds that have been developed on an eroded sur-



FIG. 17.—*Structure beneath the marginal terraces*

Strongly bedded ash together with associated shales cut by small dikes forming a part of the terrace near Guayama. These rocks belong to the older series and dip into or toward the mountains rather than toward the sea.

face which beveled across the more complex structures of the older series of formations that formerly made up the mass of the island. These limestone beds are several hundred feet in thickness and dip gently toward the sea. On the inner margin of their present extent toward the interior, especially along the north side of the island, they are abruptly terminated in a very irregular line of modified cliff forms facing toward the prevailingly smoother and lower ground for some distance toward the interior. For the most part, this limestone margin is exceedingly rugged and broken. The width of the belt with this rugged character

varies very much in different parts of the field. Its most striking development is in the district extending from Tao Alto to Aguadilla. In the district extending eastward from San Juan and also in some of the areas on the south side, this margin is very much broken and so obscure in some parts as to escape detection. In its best development, however, it is a typical *cuesta*, formed in the usual manner by the erosion of a formation representing a recently uplifted coastal series. The series of formations involved formerly extended inland very much farther than they do now. Only the outer margin remains from the erosional destruction of a series of beds and reefs that in former times covered a



FIG. 18.—*Inner lowland near Bayamon*

View looking north from the Bayamon-Comerio road toward San Juan, showing the monotonous features of the lowland belt in the foreground and the comparatively prominent hill remnants of the Tertiary formation *cuesta* in the background.

large portion of the island. The road running from Aguadilla to Moca, San Sebastian and Lares extends for practically the whole distance, after leaving the coast, along the inner lowland at the foot of this *cuesta* or along the cliff forming the *inface*. The same features characterize the surface topography as far east as Corozal. This feature is much less pronounced on the south side of the island.

Peneplain

Beneath the limestones constituting the *cuesta* and representing the Tertiary series there are, in numerous places, traces of a former plain that represented the results of erosion on rocks that had a complex struc-

ture. Occasional profiles of more distant ridges also show a sky line that suggests the former existence of such a plain, and in favorable localities it can be traced directly to the foot of the limestone cuesta. Occasional traces are also seen on more mountainous tracts, especially at the west end of the island, near Rincon and in the vicinity of Mayaguez. At the latter place, these remnants of the old plain are called mesas. It is the judgment of the writer that these all belong to a single base-leveling surface or marine-cut platform formed in the period just preceding the development of the Tertiary limestone series. Judging from beds developed immediately upon this surface, it must have been completed in early



FIG. 19.—*Haystack (pepino) hills*

A characteristic view, showing the small soil-covered flats and associated haystack hills found in the region of the Arecibo formation. Photograph taken on the road between Arecibo and Barceloneta.

Eocene time, and perhaps was even largely developed in pre-Tertiary time. It may be referred to as the early Tertiary base level or peneplain.

There are many minor features giving variety to the surface relief which depend for their particular relations and character on underground structures which are as yet imperfectly understood.

Haystack Hills

The most striking topographic feature of the whole island is the remarkable development of small isolated or grouped rugged hills usually rising abruptly above adjacent smooth flat soil-covered areas at various levels throughout a broad marginal belt along the north coast, west of

San Juan. They constitute a feature so unusual that even the untrained casual visitor is impressed with them.

This feature has been referred to before in connection with the description of the "Younger series" of rocks, especially the Arecibo reef limestone formation. In spite of the unusual appearance presented by this distribution of "haystack" hills and intervening flats, their origin is judged to be comparatively simple. The active agents and processes have been the same as those at work on all other parts of the island, but the results differ because of the fundamental difference of material and



FIG. 20.—*Cave structure in the haystack (pepino) hills*

Near view of the limestone hills forming the margins of the small cultivated flats in the typical haystack hills district. This view shows the cavernous nature of the limestone forming these hills, a structure that is regarded as the most significant feature and probably the largest factor in the development of these peculiar relief forms.

structure. Nowhere are these features developed except where the later reef limestones are the underlying bed-rock formation.

The essential steps in the development of these forms are the following:

The reef limestones are not uniform in composition or structure. They have more or less intermixture of earthy matters which are distributed irregularly, but chiefly at certain horizons, as more earthy or shaly beds of no very great lateral or vertical extent. Such conditions are re-

peated at occasional intervals in successive horizons. As such a series is lifted above sea level and subjected to ordinary erosion and weathering, the tendency is, (a) for the purer and more massive reef limestones to be attacked by the solvent action of percolating water with a development of underground channels, porous rock condition and actual caverns, (b) for the more earthy layers to resist and limit such action at the levels where this matter is present in sufficient abundance, with a development of residuary material. As this action progresses toward maturity, many of the larger caves collapse and sink holes are thus formed. With still further development, the sink holes merge into each other in local areas where solution has been most active, the earthy debris forms a soil in the bottom corresponding in level with the first important earthy layer, and adjacent remnants of the limestone reef stand out as sharp rugged hills separated by irregular notches that represent other smaller collapsed caves. The result of such action and conditions, finally, is the numerous "haystack" hills standing on flat soil-covered areas or surrounding such areas as if they were just set down as bunches on this surface. This relation is repeated at different levels throughout the belt from San Juan to Aguadilla, but the most striking developments are local, apparently where the structural relations are just right, and may be seen best between Tao Alto and Arecibo, especially in the vicinity of Manati and Vega Alta.

It was at first thought that former subsidence levels might have something to do with establishing the level tracts, but the observation that these tracts stand at very different levels in immediately adjacent districts together with recognition of the structural difference, lead us to give credit to the primary structural character of the formation itself as the controlling factor in the present distribution. According to this explanation, these hills are mere remnants left from solution attack on a reef limestone, the depressions between them representing collapsed caverns, the walls of which may still be seen on the sides of some of the more rugged hills, and the surrounding or intervening tracts are soil-covered and level, chiefly because of the accumulation of earthy material, left behind after removal of the overlying reef, now halted in its reduction at the first important less soluble beds.

MINERAL RESOURCES ⁶

An examination of specimens of minerals and ores in the hands of local prospectors and residents interested in developing mineral resources.

⁶ A good list or tabulation of the mineral occurrences of Porto Rico may be found in the article by H. C. B. Nitze listed at the close of this paper.

together with observations made personally, shows that there is considerable range of minerals and ores. It appears also that considerable attention has been given in a few cases to local development. There is large variety shown in a collection of this material and in some cases the specimens exhibited look very promising indeed. But there is almost no reliable information touching the quantity or the exact relations or estimates of possible profitable development. It can be said, without danger of contradiction, that none of the developments so far undertaken looking toward the systematic mining have proven profitable.

Gold

Only one enterprise of this kind seems to furnish any production, and this is the placer mining for gold. Gold washing has been practiced from the early Spanish occupancy to the present time, and it is not at all a rare thing to see several men digging in the stream gravels for the "pay dirt" and panning out the gold. This is done in all cases on a very small scale and with the aid of the simplest equipment, and the returns appear to be very moderate. It is claimed that in former times a much more elaborate system of working such deposits was in operation under the Spanish regime, and, according to historical statements, they were considered profitable. More recently, there has been at least one attempt near Corozal to develop this kind of ground by the use of modern appliances, but the plant has been allowed to go to entire ruin. The only places where actual placer washing was seen in progress was three miles south of Corozal and on the Sabana river near Luquillo. Near Corozal, also, some work has been done in an attempt to discover the veins or lode which may have furnished the placer gold. There are several pits, trenches and shafts, in some of which quartzose stringers were seen which appear to fulfill the requirements of a source of supply. Some free gold was found in panning a little of the weathered material at one of these spots. There is little doubt but that these veinlets or stringers, which were numerous at one of the cuts, are in part the sources of the placer gold of this locality. But at no place examined was there to be seen any "vein" of apparent consequence or any structure suggesting the course or extent of the mineralization. Of course the rather mixed state represented by the residuary matter, seen almost everywhere at the surface, does not lend itself readily to the tracing of veins, and it may therefore happen that conditions would prove, after thorough exploration, to be better than the first brief examination indicated. There are said to be some old abandoned workings dating back to Spanish conquest times at

the same locality, but such evidences are very obscure and would seem at best to have very little bearing on present prospects.

Copper

Some very good specimens of copper ores were seen in the possession of Mr. Henry D. Sayre, of Corozal, who assured us that there were several localities represented in the collection and that in no case had the real value of the occurrence been determined. It was understood that examinations have been made by engineers sent to Porto Rico in the interest of American mining companies, and that some exploratory work has been carried on by Porto Rican companies or groups of individuals, but so far as known there is at the present time no development work being conducted, and the possible value of these deposits has not been thoroughly proven.

Zinc, Lead and Silver

One prospect, on which several hundred feet of underground work has been done, was visited at Barrio del Carme in the Sierra de Cayey, on land owned by Pablo Vasques, several miles northwest of Guayama. The country rock is chiefly andesitic tuffs cut by porphyritic intrusives. A quartz vein carrying sulphides, pyrites, sphalerite, galenite and chalcopyrite has been followed and there is some ore on the dump. The vein varies from a mere streak to a width of two feet. The mineralization is irregular and the values are said to be chiefly in lead and silver. The second-class ore is essentially mineralized tuff. The exploratory work has been done in large part on side slips and streaks quite outside of the vein proper. In all of this side work, there was apparently no new mineral-bearing ground discovered. The first-grade ore is heavy and the distribution of values is not determined. There is no doubt of the existence of a real vein or of the ore in this case, but there is need of more intelligent exploratory development along the vein proper, together with a study of the possibilities of separating the chief values by some sort of milling operation, before a reliable conclusion could be reached as to possibility of working the deposit as a mine.

Iron

One magnetic iron prospect was visited. This occurrence is on the divide about ten kilometers west of Naguabo. It is reached by driving out on the road from Naguabo toward Torres to about this distance and then taking saddle horses to the divide, a distance of about two kilometers southward. On the expedition we were accompanied by Mr. Arturo Gallardo, Jr., Alcalde Municipal of Naguabo.

There are many surface boulders of magnetic iron of fine quality in this vicinity. A little underground working is evident at one point but this is now caved in. Surface observations, together with a few magnetic observations, failed to show any very extensive deposit at that point, but the quality appears to be good in iron content. The ore carries a little copper and is associated with an igneous rock essentially andesitic in composition. It could be traced with a fair degree of certainty about fifty feet east and west just below the crest of the ridge. Considering the associations at this place, it seems necessary to conclude that the ore is igneous in origin and that it probably accompanies one of the porphyrite intrusives. Other occurrences of similar ores were mentioned to us in this same region, but none were visited.

Coal and Oil

There is no good ground for believing that valuable resources of these products exist in Porto Rico. Some prospecting for them is carried on, however, in a desultory way. The only basis for the hope of finding coal is the occurrence of lignite and lignitic material with the shales lying at the base of the younger series of rock formations, below the Arecibo limestone member. Lignitic material was seen in these shales near Lares, and similar or better material has been reported from near San Sebastian. From what has been seen, there seems to be no promise of very valuable deposits of this kind. The structure is simple and a very little exploratory work done in a systematic manner would determine the probable value of every occurrence known. There is no promise at all of such content in the older series.

No oil indications were observed. The only formation to be considered in investigating the prospect of oil is also the basal shales of the younger series.

Limerock

A particularly porous, granular and uniform limerock is obtained from the small island, Icacos, just off the northeast coast, and is used in sugar refining at the Central, owned by the Bird brothers, at Fajardo. The rock is organic, largely foraminiferal, and is probably structurally of the same origin as the San Juan dune sand deposits,—comparatively recent. Such materials are doubtless to be found in large amount, but not always so pure and so uniform in quality and structure. Limestone suitable for lime burning or for cement mixture is certainly not rare. Limestone of a quality that would permit its use in structural work is also found at some places, but apparently very little native stone is used.

Guano

Bat guano is found in some of the caves in sufficient amount to be a source of local fertilizer.

Road Metal

Several kinds of stone were seen used extensively in road improvements. The particular variety used depends largely on the local supply, but the most common are the Arecibo limestone and the massive syenite and granite porphyry. There is no lack of these as well as other types suitable for such use.

There are other mineral substances that will invite investigation, but no others came under the writer's personal observation and no facts regarding them are in hand.

HOT SPRINGS

Thermal springs are known in the vicinity of Coamo. Judging from their location and apparent relation to other physical features, they are believed to lie along a fault weakness. The district is also one of comparatively late igneous activity, and this, coupled with the other factors, leads to the suspicion that the springs are directly connected with the dying igneous activity and may actually represent juvenile waters.

At Coamo Springs Hotel, one of these springs has been developed and controlled for commercial purposes. The water is hot as it comes out of the side of a small ravine and runs down over the slope, which is covered to a moderate extent with deposit from these waters. The immediate bed rock is not well exposed, but it is judged to be either a tuff or an igneous complex and the field relations in the vicinity show that there is a thick series of beds both above and below. No doubt critical field study could determine the actual relations with considerable certainty.

An analysis of these waters, furnished by the proprietor of the springs and made at the agricultural experiment station at Mayaguez, is as follows:

Fixed elements per litre of water

Free carbonic acid.....	0.01296
Sulphate of lime.....	0.79902
Sulphate of soda.....	0.52531
Chloride of potassium.....	0.00031
Chloride of sodium.....	0.23054
Silicate of soda.....	0.08127
Carbonate of soda.....	0.03503
Carbonate of iron.....	0.01114
Total.....	1.68559

Gases in solution per litre of water at 0° of temperature and 760 mm. of pressure

Nitrogen	13 cc.	740
Oxygen	1	761
Sulphydric acid.....	1	967
<hr/>		<hr/>
Total.....	15	2468

HISTORICAL STATEMENT

A complete or even a reasonably full account of the geological history of Porto Rico cannot be written at this stage of the investigations. Such a statement is necessarily the end product or climax of the whole series of studies that are proposed, but it may not be out of place to outline some of the leading and most clearly marked steps as a rough sketch or a preliminary attempt.

At the outset, it is well to appreciate that the Island of Porto Rico is geologically young. There are no traces, so far as known, of any of the so-called ancient rocks. It is quite true, of course, that the older series of formations is largely a volcanic complex whose exact age may never be accurately determined, but there is no occurrence of profoundly metamorphosed members or other evidences of great geologic age. Besides, the series, complex as it is and difficult to group into suitable divisions as it may be, undoubtedly forms a very closely related succession of minor formational units whose uppermost members are determinable as to age with reasonable accuracy. It would appear also from the nature of the deposits and their structural relations that the accumulation must have been, for the most part, a rapid process.

There is no good reason, so far as any of these facts are concerned, why the whole of the "Older series" could not have been accumulated in a single geologic period. The fossil content of the upper members of this series indicates that this period was the Cretaceous, as used in the broader sense in geology. Whether or not the older members date back to an immediately preceding time cannot yet be definitely stated, but whatever there is, is clearly so closely associated with the Cretaceous beds that they can all be treated as a single historical unit.

This earlier period is characterized by volcanic and other igneous activity on a very large scale. Beds were accumulated both above and below sea level. There seem to have been oscillations of level accompanied by recurrences of similar beds, and apparently much shifting of the supply of material accompanied by great variation of character laterally. There is good evidence that succeeding volcanic outbursts broke through these beds at many places.

An occasional more prominent change of conditions, more or less clearly marked in the structural relations and character of material, may possibly be used as a basis for epochal subdivision. It is quite clear, however, that there was no profound change of geologic control throughout the whole of this earlier time,—it was strictly a volcanic period. The succession of disturbances by which it was affected is represented in part by dynamic modifications of the nature of folding, crushing and faulting, but this is probably an accompaniment of the more profound igneous activities also, and need not be regarded as evidence of any strikingly different causal process. If there were contributory causes of a regional sort controlling the folding, they are essentially simply superimposed upon or introduced into the larger, more profound and longer continued igneous activities which prevailed both before and after that time.

This long period, characterized by great complexity of formational development, including tuffs, agglomerates, conglomerates, shales, limestones and immense numbers of intrusives of great variation in size, form and composition, finally came to an end by the dying out of the volcanic energy, and greater stability of the whole with respect to elevation and subsidence was established. Erosion cut down the exposed formations, the sea attacked the margins and in time most of the projecting mountain mass was reduced near to base level, the sea encroached far onto the former land areas and a new historical chapter was begun.

It is not possible to say, with the data in hand, that the entire island was reduced to a peneplain, or perhaps a conoplain, but there is good evidence, from the traces still left of former planation and from the disposition of the remnants of overlying formations still preserved, that the greater part of the present area was worn down to base level and submerged. The process of base leveling was going on before the close of igneous activity and it was continued long enough to bevel across rocks of all sorts with marked success, but there is no necessity for regarding it as a very long geological time.

As erosion proceeded, sediments were deposited unconformably around the margins of the island of that time and perhaps also in some of the marginal valleys above sea level. These constitute the earliest shale beds of the "Younger series" and are believed to be of Eocene age. They are at least early Tertiary. Where more simple marine conditions came into control, as would happen when submergence or planation had masked or destroyed the more elevated sources of supply, the deposits became almost wholly reef limestones and shell limestones, with only minor amounts of strictly detrital material irregularly distributed. This gave a succession of somewhat irregular beds which are abundantly supplied with organic

remains and which bear evidence of the continued depression favorable for the growth of these accumulations for a considerable part of Tertiary time. There is some suggestion in the relations shown in the eastern portion of the island that this end was not wholly submerged and that differential subsidence gave to this portion less prominent development of the heavy, massive limestone beds.

In later Tertiary time there was marked reëmergence from the sea, accompanied by warping, so that the later limestones and reefs were lifted to very different elevations in different parts of the island margin. Since that event, the whole has been again subjected to erosional attack of the sea, and to wind work, with the result as now seen in the physical features. The comparatively easily destroyed shales, marls and limestones of the Tertiary series have been extensively removed, leaving only a fringe of these formations along the north coast and a part of the distance along the south coast, and developing all of the topographic forms characteristic of the erosion of emerged coastal deposits, together with some very special forms due to the peculiar makeup and attitude of the rocks themselves.

Since this first emergence there have been minor oscillations also, the record of which is observable in marginal terraces, deeply trenched flood-plain deposits, and thoroughly indurated wind deposits of presumably Pleistocene age. Apparently the latest movement has been one of slight emergence.

A summary, therefore, of the larger items in the geologic history includes the following:

- 1) A long geologic period of volcanic activity, accompanied by marginal attempts at assorting of fragmental and detrital material and organic accumulation disturbed from time to time by renewed or extended igneous activity.

- 2) A dying out of volcanic energy, greater stability of the mass with respect to elevation and subsidence, and erosional attack continued long enough to result in extended planation and partial base leveling with final extensive submergence.

- 3) The development of an unconformable overlying series of shales, reef limestones and related deposits chiefly of organic origin, brought to an end by final re-emergence.

- 4) The development of present surface features under stream erosion and marine marginal attack, with modifications arising from oscillation of level.

The geologic column forming the basis of this outline, avoiding minor details that are properly the subject of further study before specific statement should be made, is as follows:

Recent alluvial deposits.

Submergence with flood-plain deposits.

Younger Series.

San Juan dune sands (Pleistocene).

Submergence with terrace cutting.

Post-Arecibo emergence and erosion.

Organic limestones, marls etc. (Mid-Tertiary).

Arecibo reef limestones (Oligocene).

Lares shales etc. (Eocene ?).

Marked unconformity.

Older Series.

Interbedded limestones, tuffs and shales etc. (Cretaceous), Coamo tuff-limestone, Trujillo Alto limestone, Aibonito conglomerates and shales with many intrusives.

Interbedded foraminiferal shales and ash shales with tuffs, cut by many intrusives (Early Cretaceous ?), Fajardo shales, Mayaguez shales, Barranquitas shaly limestones, Sierra de Cayey tuffs, Comerio consolidated ash beds and tuffs, etc.

FUTURE PROBLEMS

One of the objects of this exploratory study was to discover and define the problems that should be investigated by this organization. It is not supposed, in enumerating this list, that these cover every possible subject of special study, but they do indicate the fields in which there is promise of immediate and valuable scientific returns, and at the same time will add to the fund of usable information to be put within reach of the people of Porto Rico.

BASE MAP

One of the fundamental things as a basis for all sorts of detailed geologic work is a good contour map. The whole island ought to be mapped in the same manner as is done in the United States, using the same quadrangle system. On account of the density of population, the complexity of structure and relief and the variety of agricultural uses of the soil, the scale should be approximately one mile to the inch, or 1:62500, so that these maps could be used as base maps for all sorts of special purposes.

The maps now available are chiefly those of the Interior Department of Porto Rico, made to illustrate the various reports of the department and representing the progress of public works such as railways, telegraph and telephone lines and highways. On account of the care with which the different classes of roads have been shown, and the general accuracy of locations, these maps are especially useful in the present investigations. One of the most useful is a map of the Bureau of Public Works

on a scale of approximately $\frac{2}{3}$ inch per mile which has even the kilometer distances along the roads indicated. Until some sort of a contour map can be secured, such maps as these will be found eminently serviceable.

Along the south coastal margin within the region of irrigation developments, there has been some special mapping with contours. In no case do they cover much ground beyond the outer lowland and terrace border, and because of this limitation they are not so generally useful for our purpose as the Interior Department maps. They are, however, very much more accurate and detailed and for the territory covered are eminently suitable as base maps.

GEOLOGIC MAP

A geologic map of the island should be one of the results of this series of studies, whether a relief map is secured or not. Such a map of the whole island is necessarily an ultimate rather than an immediate product, but district maps can be undertaken at once, with no difficulty whatever. These preliminary districts can be selected so as to include some of the most promising investigation problems in special lines, and both kinds of work can thus be carried on at the same time. This therefore leads directly to the next item, which is district studies.

The only geologic map thus far attempted is that by R. T. Hill.

DISTRICT STUDIES

It is possible now to select areas which are known to contain geologic features of special interest and significance, and it will generally be convenient, if not indeed necessary, for the investigator to make a detailed geologic map as a secure foundation for his special studies. One of these is the Coamo Springs District, which may be made large enough to extend from the Descalabrado river on the west, to Salinas on the east, and reach as far north as Aibonito. It will include as features of special importance for investigation, in addition to the mapping, the hot springs, the great conglomerate series, one of the later of the great volcanic vent complexes, the genetic history and horizon of the Coamo limestone which is a striking mixture of volcanic and organic matters, the high floodplain deposits of the stream valleys and their bearing on late geologic history, and certain physiographic studies connected with the coastal terraces. This district promises, as can be seen, an unusually large range of topics inviting special study, all of which will be illuminating to further development of the geologic survey of the island.

Another district of equal promise in a very different manner is on the north coast extending from the Quebradillas to the Arecibo river and

reaching from the sea to Lares so as to include a strip of the older complex rock series beyond the inner margin of the Tertiary series of reef limestones and shales which constitute the greater part of the bed rock of the area. Beside the mapping and detail of structural relations, this district presents the best opportunity to investigate the question of exact age of the basal beds of the Tertiary series, the transition from lignitic shales of perhaps fresh water alluvial origin to massive limestones of reef type, a subdivision of the Tertiary series, the meaning of the thinning out and disappearance of the Lares shales toward the east, and a paleontologic study of the beds, all of which are fundamental in any additional study of other districts containing the Tertiary rocks. There are besides good opportunities to study the meaning of the high terrace-like shelf coming abruptly to the sea at Quebradillas river and the meaning of the deep embayments now occupied by such playas as that at Arecibo. This is also one of the best localities for a detailed study of the structural and petrographic features of the San Juan formation as well as the behavior of modern dune sands along the present coast.

Another district of still different features, and giving foundation for special studies of quite a different bearing, is that lying between Caguas and the Caribbean sea and perhaps extending as far eastward as Naguabo. This will include the largest massive igneous unit in the whole island and promises information bearing upon magmatic differentiation, origin of the magnetic iron ores, relation of the great intrusive masses to the other igneous representatives, petrographic range of the igneous rocks, and marginal metamorphic or other effects,—studies fundamental in a final statement of the igneous history of the island.

There are other districts which have special problems associated with the regular areal geologic work, but these are sufficient to indicate the range of such district studies and their variety.

Certain special investigations are of a sort requiring comparison and summary of many different localities, and for these it will not be wise to handicap the investigator by limiting work to a single district. Some of these are suggested below.

REEF-BUILDING ORGANISMS

The limestones of Porto Rico are remarkable for the great prominence of algæ and corals and other closely associated organisms lending themselves to the construction of reefs and accompanying deposits. These forms belong to practically every limestone formation of both the older and the younger series except those most closely related to the shales. It is a study requiring the training of a specialist in such lines.

PALEONTOLOGY

The total organic content is much greater than is intended to be included under "Reef-building organisms." There are immense numbers of splendidly preserved fossil species of organisms belonging especially to the Tertiary series. Probably a great many are new to science. There are probably few places in America or within territory belonging to the United States where the marine Tertiary succession is of more promise than in Porto Rico. This problem or line of investigation is closely related to the next topic, that of Tertiary subdivision.

TERTIARY SUBDIVISION

A faunal and structural summary will naturally lead to the establishing of subdivisions and the determination of horizons in the younger series of rocks culminating in a statement of the complete Tertiary history of the island.

SAN JUAN FORMATION

A study of the characteristics and detail of origin and historical steps associated with the Pleistocene fossil dune sands, referred to as the San Juan formation, is another problem.

SUBDIVISION OF PRE-TERTIARY COMPLEX

A discussion of this kind is one that will properly follow upon the completion of areal work in several of the typical districts. It is, however, one that will necessitate investigations throughout the interior of the island, and will include a summary of the characteristics of all of the prominent local formations. A grouping and correlation can no doubt be made in due time.

MINERAL RESOURCES

On account of the interest taken by the people of Porto Rico in the question of possible mineral resources, it is desirable to undertake an investigation of the kinds of products, their origin, distribution and probable economic value. In connection with this, because of the small amount of exploratory work that has been done, it would be especially useful if suggestions were made at the same time about the methods of exploratory development and the people cautioned concerning wasteful methods. This work should be done so as to cover the whole range of mineral possibilities in the island regardless of location. There are known deposits of copper, iron, gold, lead, silver and zinc among the

metals as well as a number of non-metallic products. But in no case is the real value, or the probable extent or the geological relation, known sufficiently well at the present time to serve as a basis for a discussion. This should be one of the first undertakings of this survey, both because of the fact that its value is fully appreciated by the people of Porto Rico and because its conclusions do not materially depend upon the other investigations or mapping progress.

PETROGRAPHY

On account of the great number of igneous rock occurrences and the very great variety that is certain to be shown in quality and minor petrographic character, and because of the considerable range in composition already known to characterize the intrusives, there would seem to be an ample and promising field in this line for a special investigation. It is possible that some genetic relationship is exhibited in the distribution of these variations and that a thorough comprehensive study would throw some light on the more obscure problems connected with the genesis of igneous rocks. This is a problem that can be taken up at any time, and that need not be regarded as dependent upon special district studies, although it is evident that the finishing of work on certain districts would facilitate a study of this kind.

PHYSIOGRAPHY

Enough is known of the physiographic features and their meaning to appreciate that a great deal of the detail of the later geologic history of the island is more or less intimately bound up in the physiographic development. The broader or larger physiographic features have already been suggested, but there are certainly many details, some of which may well be of much significance in understanding the geologic history, which will require the special attention of a trained physiographer. Porto Rico is a unit of geologic history, of geologic structure and of physiographic form. Each is of sufficient complexity and unity to be made independent subjects of investigation.

THERMAL WATERS

The hot springs in the vicinity of Coamo Springs suggest from their situation and reported composition the possibility of being representatives of juvenile waters. It is believed that a study, planned especially to investigate the origin and character of these waters, together with such others as may exist, would be a very suitable special investigation. On

account of the fact that the principal occurrence of this type of water is very local, it would be possible to combine a study of this kind with a district study such as has been referred to in a preceding paragraph.

GEOLOGIC HISTORY

The complete geologic history of the Island of Porto Rico cannot be written until all of these and perhaps other more special investigations have been made. A complete historical statement must be regarded as an end product of the whole range of studies carried out for more special purposes. It is, therefore, the final topic and may well be deferred to a time when most of these already suggested have been carried far enough so that the data of special importance secured by them are available for this general summary.

It is evident from the appearance of this list that there is a very great amount of geological work awaiting the investigator in Porto Rico, and that it is varied and complicated enough to require several years of study in large part by experts or specialists in all branches of the subject. It can be seen also that the Island of Porto Rico is a geographic unit of more than usual complexity and scientific interest and gives promise of results for effort expended in researches along geologic lines.

COLLECTIONS

A beginning has been made toward securing a representative collection of typical rocks and fossils. Several hundred specimens were brought to New York for use in formulating the accompanying description, and as a possible basis for further more special investigations.

As a first step in this direction, about a hundred thin sections of the rocks have been made for microscopic study and detailed comparison. They will form a basis in planning the special petrographic investigations which may be undertaken.

In like manner a large number of fossils have been gathered and their general relations are being studied. Additional investigations along paleontologic lines will be in large part outlined or suggested by the trend of these studies, for although the collection is very fragmentary it is nevertheless characteristic and fairly representative of the principal formations.

More than a hundred photographs were taken of strictly geological subjects illustrating typical physiographic features, structural detail of rock formations, structural relations, etc. These are all suitably labeled and form the beginning of a collection of illustrations of Porto Rican

geology. In addition to the regular photographs, a number of photomicrographs have been made from the thin sections of typical rocks.

Some of this material will finally serve as a foundation for the geological section of what it is hoped may become a Natural History Museum of Porto Rico.

ILLUSTRATIONS

CROSS-SECTIONS

The note books of the party and field maps carry a record of field determinations and detail of structural relations and comments greatly in excess of what can be published in such a report. They are the property of the organization and are of particular service as guides in planning further work and in giving each new investigator his bearings, together with some suggestions about the character of his own district or the distribution of data bearing upon his special investigation. The note books contain observations along some of the principal roads in sufficient detail to serve as a foundation for complete generalized geologic cross-sections of the island on two especially important lines.

Cross-sections, therefore, have been drawn to illustrate the kind of surface relief, the grade of the road, the kinds of rocks or rock formations and the geologic structural relations, and are reproduced to accompany this report. An immense amount of detail is necessarily omitted or combined into generalizations in order to bring the sections within the scope of a publication of this kind. It is judged that some of these details will be suitable illustrative matter for future reports based on studies of special districts. One of the sections is based on data gathered along the road from Ponce to Arecibo. The line is drawn from Arecibo to Ponce direct and the data are projected to this line. This method tends to obliterate the windings of the road and secure practically normal proportions and relative positions for the associated formational units. The other section line is drawn directly from San Juan Point to Santa Isabel. By projecting to this line all the data gathered on the Bayamon-Comerio-Barranquitas-Coamo road a great deal more elimination of road curves is accomplished than in the other section, and it makes the grades of the road look somewhat abnormal by reason of this shortening of road distance of certain large curves, but on the whole the relations are shown without special difficulty except that attendant upon the need of generalizing the minor structural detail.

MAPS

A hasty reconnoissance examination is seldom a satisfactory basis for an areal map. This is quite true of the present investigation. On this account, therefore, if it were not for other considerations, an areal map would not be attempted. But in this case, where a good many more or less independent special investigations are to be carried on in which a reasonably accurate geological map will prove decidedly helpful, there is sufficient excuse for presenting a reconnoissance map. An earlier map of this kind prepared by R. T. Hill was made under conditions so much less favorable for travel, and seems to have been constructed in some particulars with so much less opportunity for observing the actual conditions in certain areas, that an entirely new map is believed to be the better solution of the present need. The accompanying reconnoissance map is intended, therefore, as a convenient guide or location map for subsequent more special investigations, and it is expected to be wholly replaced by one of much more detail and greater accuracy as a final product of this survey.

ACKNOWLEDGMENTS

The members of this expedition have appreciated the very material help, the sound advice and useful suggestions given by the officials of the government of Porto Rico, and are indebted to Governor Yeager for his very practical aid in making arrangements for the field work and for his live interest in these investigations; to Colonel Shanton, chief of the Insular Police, for his willingness to give introductions to men acquainted with special mineral localities and for his precautions to insure protection against unnecessary delays; to Mr. Wheeler, of the Interior Department, for assistance in securing suitable maps as a basis for travel and notes; to Mr. Bonner, the Auditor, for facilitating the settlement of accounts; to Dr. Lippitt, of the Bureau of Sanitation, for information regarding sanitary precautions and hotel accommodations; and to Mr. Campbell, of the Bureau of Transportation, for the excellent equipment for travel which contributed largely to the success of the expedition.

Many others have been of assistance in pointing out localities of special interest, in giving names of reliable informants and in acquainting us with the usages and customs of the country.

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SAN JUAN

Cataño

Bayamon

Guaynabo

La Mesa

Caguay

Las Cruces

Cayey

GUAYAMA

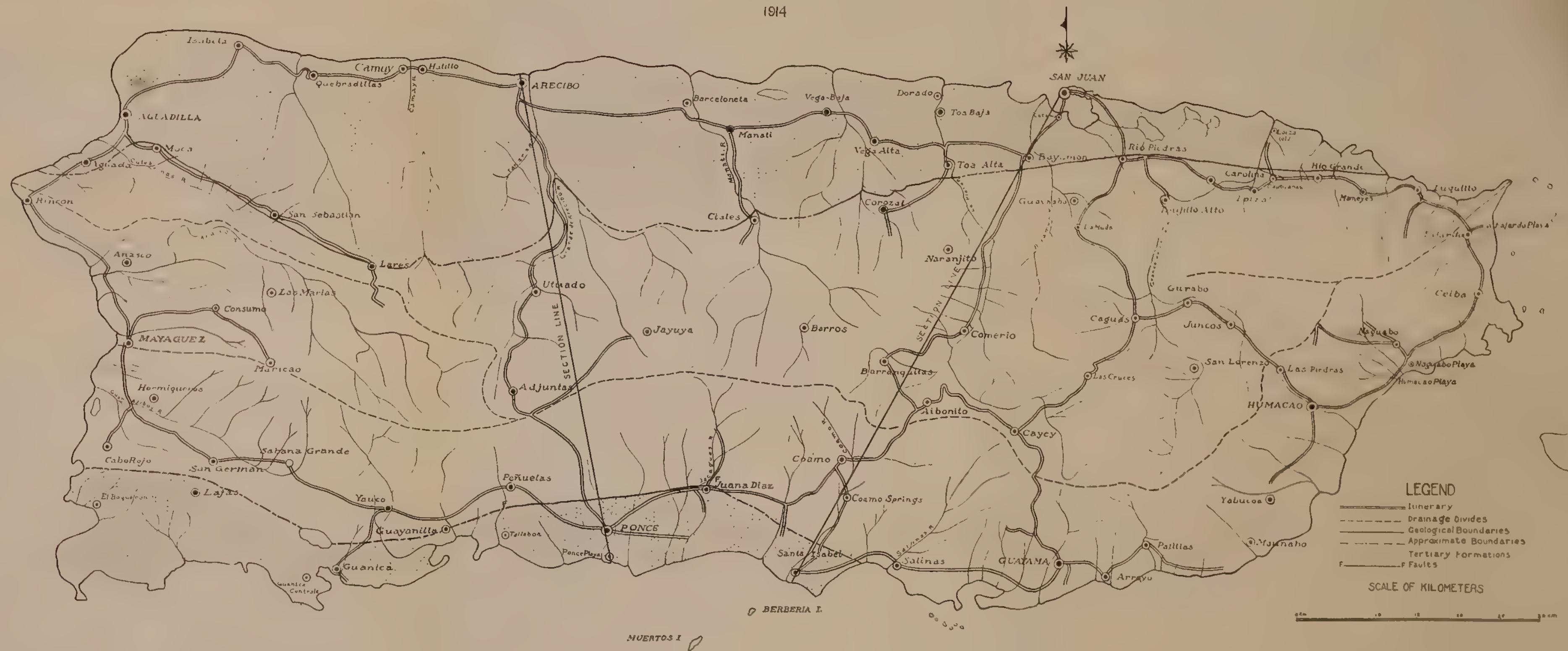
GEOLOGICAL RECONNAISSANCE MAP

OF

PORTO RICO

NEW YORK ACADEMY OF SCIENCES EXPEDITION

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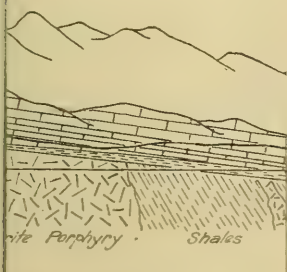
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FIGURE 1

FIGURE 2

FIG. 1.—Generalized geological cross-section of the Island of Porto Rico from Ponce to Arecibo

FIG. 2.—Generalized geological cross-section of the Island of Porto Rico from Santa Isabel to San Juan

These sections are intended to show the road profile, some of the side relief and the geologic structure. They are based on observations made along the roads and projected to a direct line. The numbers placed at the base of the sections correspond to the kilometer stations on the roads.

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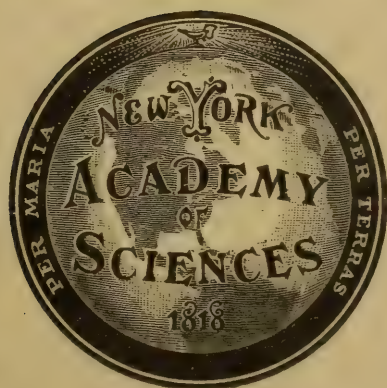
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LIST OF GREATER ANTILLEAN SPIDERS
WITH NOTES ON THEIR
DISTRIBUTION

BY

FRANK E. LUTZ



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29 MAY, 1915

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ERRATA

ANNALS N. Y. ACAD. SCI., Vol. XXVI

Page 144, first column, line 20 from top, for *coronotus* read *coronatus*

“ 144, second column, line 18 from top, for *Ellica* read *Eilica*

“ 145, first column, line 9 from top, for 60 read 101

“ 147, second column, line 10 from top, for *Salticus* read *salticus*

LIST OF GREATER ANTILLEAN SPIDERS WITH NOTES ON
THEIR DISTRIBUTION ¹

BY FRANK E. LUTZ

(Presented by title before the Academy, 12 April, 1915)

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INTRODUCTION

The principal general lists of Greater Antillean spiders are by Nathan Banks, who has reported on collections from Cuba (1909), Haiti (1903) and Porto Rico (1902). Practically the only list for the Lesser Antilles is Eugène Simon's for St. Vincent. Except for Banks's Cuban list, which was overlooked, A. Petrunkevitch (1911) has included nearly all the published records. For the sake of uniformity I have followed rather closely his synonymy even though it is not, in all cases, in agreement with the ideas of Mr. Banks, who is responsible for the identification of most of our specimens. Unless otherwise stated, I have also relied on Petrunkevitch's catalogue for data concerning distribution in the western hemisphere. I have usually departed from the alphabetical arrangement of genera used by Petrunkevitch and followed more nearly the arrange-

ment of Simon's *Histoire Naturelle* (1892-1903) and have relied largely upon Simon for data concerning distribution in the Old World.

The dissertations on distribution have been included because a study of the problems of distribution is the main excuse for a faunal list. I well realize that we know far too little of the fauna of this and neighboring regions to attempt to draw final conclusions and I also realize that even if our knowledge of the spiders were perfect it would be necessary



FIG. 1.—View of a portion of Mona

Nearly all of the specimens referred to in this paper came either from the grassy portion of the coastal strip (shown in the foreground) or from the thicket at the base of the cliff.

to study, in connection with their distribution, the distribution of other organisms, especially those of which we have more geologic records, but it seems that we have now a basis for an interesting discussion at least.

The new records in this list come mainly from four sources, the specimens being in the American Museum of Natural History: collecting in Cuba in September and early October, 1913, by the author and Mr. C. W. Leng; in Porto Rico, Mona (Figure 1) and Desecheo (Figure 2) in February and March, 1914, by the author; in Jamaica in February and

March, 1912, by the late Mr. J. A. Grossbeck; and in Culebra and Porto Rico by Professor Wm. M. Wheeler. The first two collections were identified by Mr. Nathan Banks. Such of the last two as have been worked up were largely identified by Dr. Alexander Petrunkevitch. Although all of these expeditions were primarily for insects, careful field notes accompany most of the spiders, and these, when deemed important, have been incorporated here.

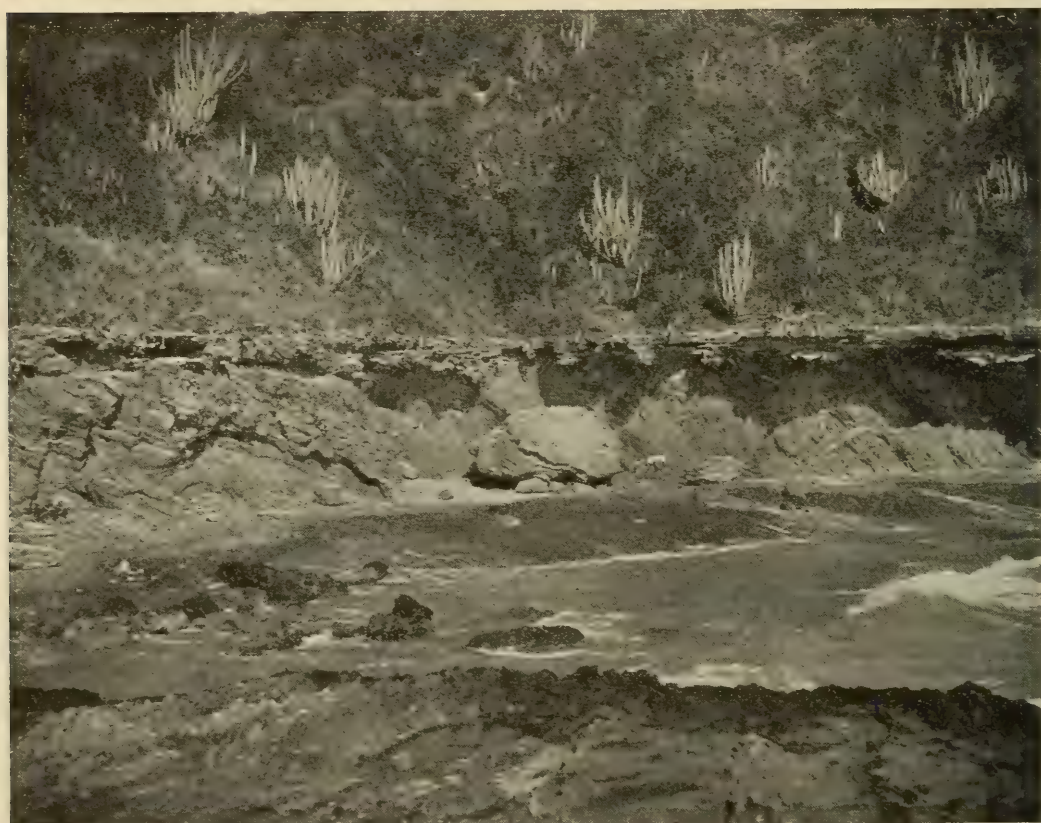


FIG. 2.—*View of a portion of Desecheo*

Unlike Mona, Desecheo has no coastal strip. The cliffs, however, are not as precipitous as on Mona. They are, for the most part, covered with trees or a xerophytic thicket.

Where a more or less definite type locality for a species is known, it usually has been indicated by the sign † before the locality, unless it is given by the context. As far as possible, the entire range is given in every case, so that when only one locality is mentioned it means that the author knows of no other records, but frequently an inclusive term is used, such as "United States," when a number of more definite localities are known.

ARANEÆ THERAPHOSÆ

Liphistiidae is an interesting family which is sometimes and on good grounds given the rank of a suborder (Mesothelæ). It has but two recent species, both of which belong to a single genus (*Liphistius*) and are known only from the East Indies. The fact that they have segmented abdomens and that they were apparently the predominant group in America and elsewhere in Palæozoic times indicate a great antiquity. If it be true, as I believe it to be, that the West Indies share with Oceanica, Madagascar and parts of Africa and South America the honor of being preserves for ancient Araneæ, it is possible that representatives of this group may yet be found in the Antilles.

AVICULARIDÆ

This family is variously known scientifically. Unfortunately the popular name for certain of these creatures is tarantula—a term used in scientific literature for a genus of whip-scorpions occurring in the West Indies and elsewhere. It is curious that no Palæozoic remains of this family have been found in either North America or Europe. The large size of the recent forms and the undoubted age of the group would lead one to expect such fossils. Of the seven subfamilies, one (Miginæ) is confined to Africa, Madagascar and New Zealand; one (Paratropidinae) is found in the Amazon region and in St. Vincent; one (Actinopodinae) has one genus with a unique species in southern Africa, one genus in Australia and one in Central and South America. The other subfamilies have representatives in the Greater Antilles and will be considered more in detail.

Mygale is a preoccupied name but there were a number of species described under it which have not yet been placed elsewhere. Of these, *maculata* Walckenær is from Jamaica and the following were described from the West Indies: *athletica* Koch, probably an *Eurypelma*; *conformis* Koch, a *Trechona*, according to Ausserer.

CTENIZINÆ

These are the "trap-door spiders," so called because many of them close the entrance to their underground tunnels with a hinged lid.

Pachylomerus is found not only in America from the District of Columbia to Venezuela and possibly Brazil, but also in the Mediterranean region and Japan. One species is known only from St. Vincent and the only other Antillean species, so far as is known, is *nidulans* (Fabricius). It is probably confined to Jamaica where it is rather common in the

central parts of the island in places where the "soil is not exposed to the effects of the extremes of heat and moisture" (Sells).

BARYCHELINÆ

Stothis. Petrunkevitch lists two species from Venezuela and one from St. Vincent but he overlooked *cubana* Banks from †Santiago de las Vegas, Cuba.

Trichopelma has two species in Brazil and one, *nitidum* Simon, confined to Santo Domingo.

The two genera just mentioned belong to a section of the Barychelinae which are tropical American except for a genus from the Mediterranean region and eastern Africa.

AVICULARIINÆ

Ischnocolus has, according to Petrunkevitch, no representative in America. *I. hirsutus* Ausserer, recorded from †Cuba and the Bahamas, is believed by him to be a young *Lasiadora*. Banks records the genus from 2,800 feet altitude on El Yunque, Porto Rico.

Stichoplastus has one species recorded from each of the following: Venezuela, Trinidad and Guatemala. Professor Wheeler took a specimen, as yet unidentified, in Culebra Island, Porto Rico.

Hapalopinus has only one species, *cubanus* Simon, and it is confined to Cuba.

Scopelobates sericeus Simon is the only species of its genus and is known only from its type locality, Puerto-Plata, Haiti.

Cyrtopholis has one species in Mexico, two in South America, one in the Bahamas, and three in the northern Lesser Antilles. In addition, *agilis* Pocock and *cursor* (Ausserer) have been recorded from Santo Domingo; *innocuus* (Ausserer) from †Havana, Cuba; and *jamaicola* Strand from Montego Bay, Jamaica. It belongs to a group which is entirely American, as far as is known.

Eurypelma. To this American genus belong the large tarantulas—the creatures which are usually thought of when the latter name is used. Only one species has been recorded from the West Indies. It is *spinicrus* (Latreille) from Cuba and is fairly common there. Banks states that he has seen an immature *Eurypelma* from Cayamas, Cuba, which represents another species but was unable to place it. The other thirty species are found chiefly from southwestern United States to northwestern South America.

Avicularia is largely confined to South America, there being one species reported as confined to California, one to Panama, three to the

Antilles and fourteen to South America. Of the Antillean species, one is recorded only from Guadeloupe and Martinique while two, *casia* (Koch) and *læta* (Koch), are known only from Porto Rico. Banks recorded *læta* from Culebra and Utuado,² Porto Rico.

Phormictopus cancerides (Latreille) is the type of a genus the only other known species of which is probably found in South America. *P. cancerides* is reported from Brazil, †Santo Domingo, Culebra,³ and the following Porto Rican localities: Lares, Anasas, San Juan. Hacienda Esparanza and Isolina.

DIPLURINÆ

Diplura macrura (C. Koch) is spoken of by Simon as confined to †St. John. Banks records it from Piñar del Rio, Cuba, under the name of *Ischnothele*. The remaining members of the genus are from South America and three closely related genera are confined to that continent. Two other genera are found in South America and also in Madagascar and Australia, one of them reaching even parts of Asia and Africa.

Ischnothele digitata (Cambridge) is recorded from Mexico and †Guatemala. It is said to live "in holes in the ground, near which it makes small, strong, irregular webs, consisting of various floors or chambers." Mr. Grossbeck took it near Cinchona, Jamaica, under a rotten log. In America the genus is reported from Mexico to Bolivia and also in the Bahamas. Either it or a closely related genus, *Thelechoris*, is found also in Madagascar, East Africa and India. Of the group of genera to which it belongs, another is American, two are confined to Australia, one to New Zealand, one to New Caledonia, one to the Trans-Caspian region, and one is found in Spain, Malasia and New Zealand.

Although *Accola* is not known in the Greater Antilles, its distribution is worth mentioning, namely, St. Vincent, Venezuela and the Philippines. A closely related genus is confined to the Fiji Islands.

Atypidæ is a small family which ranges over much of the warmer portions of the northern hemisphere and is even found in Argentine and Malasia. It is not known from the Antilles.

ARANEÆ VERÆ

The Hypochilidæ are undoubtedly Araneæ Veræ but they differ from other members of this suborder and agree with the Theraphosæ in the

² The spelling throughout this paper (Proc. U. S. Nat. Museum, XXIV, 1902) is "Utado." Doubtless the place now known as Utuado is meant.

³ This and the Porto Rican records are given by Banks under the name of *Schizopelma erichsonii* (Latreille).

possession of two pairs of book-lungs. There are but three species according to Comstock, one in the mountains of Tennessee, one in China and one in Tasmania.

ULOBORIDÆ

Like the Argiopidæ, the members of this family spin orb webs but the webs contain a hackled band not found in those of the Argiopids. The spiders themselves differ in important anatomical characters. Three of the five American genera occur in the Greater Antilles.

DINOPINÆ

Dinopis is found in Africa, Madagascar, Australia and certain of the Pacific Islands. Of the eleven American species, two are recorded only from Mexico and Central America: seven from South America; and one, *spinosa*, from southeastern United States, Venezuela and St. Vincent. *D. lamia* MacLeay is recorded from †Cuba. The only definite localities given in this island are Santiago de las Vegas (sweeping grassland) and Cayamas. We took it on the steep rocky coast of Desecheo by beating low shrubs. *Dinopis* belongs to a subfamily of which the only other genus is found in Africa, Australia and New Caledonia. It is evidently an old group.

ULOBORINÆ

Uloborus is cosmopolitan and *U. geniculatus* (Olivier) is known from Australia, Malay Archipelago, Bourbon, Bermuda and the American tropics and subtropics. This species is recorded from several of the Lesser Antilles but the only definite records which have come to my attention from the Greater Antilles are the following by Banks: the laboratory at Santiago de las Vegas, Cuba; near Port au Prince, Haiti; and Lares, Porto Rico. It is surprising that we have not taken it in the Greater Antilles. It is usually found about houses and its webs are frequently conspicuous by reason of star-like egg-sacs fastened to them. *U. americanus* Walckenær is widely distributed in the western hemisphere but is more northern in its distribution than *geniculatus*. We have it from Labrador and it is known throughout the United States and south to Costa Rica; also in the Bahamas. The only definite Antillean record I have seen is that by Banks, under the name of *plumipes*, from Cayamas, Cuba. *U. republicanus* Simon is known from †Venezuela and Cuba. We took it at the edge of a mangrove swamp near Cabañas, Cuba, and observed the same habit noted by Mr. Schwartz (1904) at Cayamas, Cuba. He says: "Each spider has an individual web, but all are placed in a great communal web, one of which was 7 to 9 feet wide, 5 to 7 feet high,

and 3 feet in depth. The male spiders were in one of the lower corners of this common web." There were about 1,000 spiders in this web and several other smaller ones had about 300 spiders in each. Of the remaining American species of *Uloborus*, one is confined to California, nine to Mexico and Central America and fourteen to South America.

MIAGRAMMOPINÆ

Miagrammopes is known from Africa, Madagascar, southern Asia and Australia. It has two species in Mexico, one in Guatemala and four in northern South America. Banks recorded the genus from Haiti on the basis of an immature specimen which could not be placed in a given species. He also described *cubanus* from Cayamas, Cuba. The remaining species is *scoparius* Simon, which is recorded only from St. Vincent but which we took near Arecibo, Porto Rico, and on Desecheo. In both these places it was among shrubs and low trees. This genus belongs to a subfamily which contains but one other genus (*Hyptiotes*) and it is northern in its distribution, being known only in Europe and America north of Mexico except, possibly, for one species from Ceylon.

DICTYNIDÆ

This family is represented by about a hundred species on the American mainland but seems not to have been reported from the West Indies. We took an undetermined species of **Dictyna** at Guane, Cuba. This genus is found in Europe and the Mediterranean region, northern and central Asia, Japan, the Philippines and from the extreme northern to the extreme southern parts of America. In America it is rather northern in its distribution, twenty-two species being known north of Mexico as compared with thirteen in South America.

ŒCOBIIDÆ

This family contains but one genus, **Œcobius**. It is known from the Azores, Canaries, the Mediterranean region, Arabia, Japan, New Caledonia and America. Three of the five American species are apparently confined to South America; one to Florida; and the fifth, *parietalis* (Hentz), is recorded by Petrunkevitch from Massachusetts, Florida, †Alabama and Lower California. Simon makes this species a synonym of *navus* Bl. and records it from the Atlantic islands, Japan, New Caledonia, Venezuela, southern United States and the Antilles. I do not know the basis of the last locality. He says it is undoubtedly carried by commerce. We took it under the loose bark of a stump on the coastal

flats of Mona. In the United States it lives in crevices of walls, especially those of buildings.

FILISTATIDÆ

This family also has but a single genus, **Filistata**. It is found in the Atlantic islands, Mediterranean region, Africa, central Asia, Philippines and Australia. In America one species is reported from the Galapagos Islands, one in Peru, one in Guatemala, one in Mexico, and a fifth, *hibernalis* Hentz, from †southern United States south to Brazil, Paraguay and Argentina. This species is known also from Bermuda; Jamaica: Havana, Santiago de las Vegas, and Cayamas. Cuba: Isle of Pines; San Juan, Porto Rico; and St. Vincent. We took it at Baños San Vincente, Cuba. It lives about houses and under stones.⁴

The families of true spiders thus far considered are provided with cribellum and calamistrum. Those which follow lack these structures.

SICARIIDÆ

This family is also called Scytodidæ. The six genera are so distinct that Simon considers each to be a separate subfamily.

Drymusa has but two species. One is known only from Cape of Good Hope and the other, *nubila* Simon is recorded only from St. Vincent. We found it fairly abundant under bits of wood and stone on Mona.

Scytodes is distributed throughout most of the world including Madagascar and Polynesia but apparently not Australia. Some of the species, normally living under stones and logs, have taken to living about buildings and have probably been transported by man. *S. bajula* Simon is recorded from Mexico; †Venezuela; Havana, Cuba; and St. Vincent. *S. fusca* Walckenær has been reported from Bermuda; Mexico to †Guiana and Brazil; Havana and Santiago de las Vegas, Cuba; Haiti: a cave near Pueblo Viejo, Porto Rico; and St. Vincent. We found it under fallen leaves in a mangrove swamp near Cabañas, Cuba, and under bits of wood on the coastal plains of Mona. *S. lineatipes* Taczanowski is known from Mexico, †northern South America and St. Vincent. We took it in weedy vacant lots at Santiago, Cuba, where it had probably been brought by commerce. *S. longipes* Lucas is found on Bermuda; Bahamas; †Mexico to Brazil and Paraguay; Havana and Santiago de las

⁴ Since writing the above I have heard from Mr. Banks that he has seen *F. insignis* Cambridge from Santiago de Cuba, Cuba. This is the species referred to above as being confined to Guatemala. It is not included in the discussion at the end of this paper.

Vegas, Cuba; Haiti; Lares and Luquillo, Porto Rico; and St. Vincent. We took it in a hotel at Mayaguez, Porto Rico.

LEPTONETIDÆ.

Two species of *Ochyrocera* and one of *Theolima* have been found on St. Vincent but no member of this family is reported from the Greater Antilles. It is worth noting that there are only two species in *Theolima*. One is confined to caves in the Philippines (Luzon) and the other is found under vegetable debris in St. Vincent and Venezuela.

OONOPIDÆ

This rather large family is represented on St. Vincent by fourteen species, nine genera, but there are no records from the Greater Antilles. It is found throughout most of the tropical world and invades the temperate regions to some extent. We took a number of unidentified Oonopids at Baños San Vicente, Cuba, by sifting leaves from the base of the cliffs. Sifting fallen leaves on the steep sides of Desecheo turned up unidentified species of **Dysderina** and **Opopæa** and the same method of collecting found *Dysderina* sp. in a sea-grape thicket at Dorodo, near San Juan, Porto Rico. Both of these genera have been found in St. Vincent, as well as in the warmer parts of the mainland, Africa and Asia, including the Philippines.

DYSDERIDÆ

This family has four small genera in America of which **Ariadna** is the largest and the only one known from the West Indies. This genus is recorded from the Mediterranean region, southern Africa, Japan, Sumatra, Australia, Tasmania, Massachusetts to Uruguay including Galapagos Islands, and one species from St. Vincent. *A. bicolor* (Hentz), which is found in eastern United States from Massachusetts to Alabama, was taken by us at Baños San Vicente, Cuba. Although this species is largely a "house spider" and, so, liable to accidental dispersal by man, the fact that this Cuban locality is in the interior and not along ordinary lines of travel makes it seem probable that this species is well established in Cuba. *A. solitaria* Simon is the species which has been recorded from †St. Vincent. We found it under fallen leaves in a sea-grape thicket on Desecheo.

CAPONIIDÆ

There are only three genera in this family. One genus is represented by a single species in South Africa. The other two are exclusively

American. *Caponina* has one species in Guatemala, one in Venezuela and one in St. Vincent. **Nops** has twelve species of which two are confined to Lower California, one is in Central America and Colombia, and seven are known only from South America. *N. guanabacoæ* MacLeay is known from Central America, and †Guanabacoa and Santiago de las Vegas in Cuba. *N. coccinea* Simon is recorded from Haiti and †St. Vincent.

DRASSIDÆ

Members of this large family usually live under stones, bark, or in other crevices. The American species are, for the most part, northern. It has been split up into subfamilies and these into groups, but it does not seem desirable to note these here. It should, however, be said that *Teminius insularis* Keys, which has been considered a Drassid, is now called *Syrisca keyserlingi* Simon and classed among the Clubionids.

Callilepis is found throughout much of the Old World. There is one species found both in Europe and Canada, two on our Pacific Coast, one from New Hampshire to Florida, and Banks has recently described *grisea* from a specimen which Mr. Leng beat off a pine tree on the sandy plain south of Piñar del Rio, Cuba.

Eilica cincta Banks is known only by the original material from Havana, Cuba. Of the other two species of this genus, one is found in Florida and one in Brazil.

Sergiolus has four species reported only from Canada and the United States and one only from St. Vincent. We took an immature specimen south of Piñar del Rio, Cuba. As *variegatus* (Hentz) is fairly wide-ranging and occurs in Florida, this may be the species. It should be said that the sandy plain south of Piñar del Rio reminds one very strongly of Florida.

PALPIMANIDÆ

Of the four American genera, three are confined to South America and are each represented by a single species. **Otiathops** has two species in Venezuela, one in St. Vincent and *walckenaeri* MacLeay in Cuba. We took it under fallen leaves along the base of cliffs at Baños San Vincente, Cuba. This genus belongs to the subfamily Palpimaninæ, whose range in the Old World is Africa and southern Asia.

PHOLCIDÆ

These long-legged spiders spin irregular webs, usually in dark places. They are, for the most part, southern in their distribution. All, except an Arabian genus, belong to the subfamily Pholcinæ.

Artema is a genus well separated from the rest of the subfamily and contains a small number of widely distributed, closely related species. It is found throughout Africa, including Madagascar, tropical Asia, Malasia, Polynesia, and tropical America. *A. atlanta* Walckenaer is the only American species. It is recorded from Mexico to †Brazil and Paraguay; St. Vincent; and Utuado, Porto Rico.

A group of six genera are separated from the rest of the subfamily by Simon under the name *Blechnrosceleæ*. They are all confined to tropical America except one which is found as far north as the District of Columbia and also in India and the Pacific Islands. Two of these genera, *Blechnroscelis* and *Mecolæsthus*, are found in the Antilles.

Blechnroscelis serripes Simon is recorded by him from the West Indies in his *Histoire Naturelle* but no definite locality is given. It is probably a *nomina nuda*. The other species of the genus are in Brazil and Colombia.

Mecolæsthus signatus Banks was described from specimens taken along a mountain stream in the foothills of †El Duque, Porto Rico. An undetermined specimen of the same genus was found on the moist cliffs along the road from Arecibo to Utuado, Porto Rico. The only other species in the genus is known only from Venezuela.

Modisimus and **Hedypsilus** form another group. Both are tropical American. *Modisimus* is known from Texas to Costa Rica and (*glaucus* Simon) from St. Vincent, St. Thomas, Santo Domingo and Jamaica.⁵ No definite type locality is given.

Physocyclus globosus (Taczanowski) is noted by Banks from Santiago de las Vegas, Cuba. We took it in the same island about plantation buildings at Cabañas and Guantanamo. It has been recorded from southwestern United States, Mexico, Colombia, †Guiana and St. Vincent. The genus is known also from tropical Asia and Africa.

Smeringopus elongatus (Vinson) is found in the tropics of both hemispheres but the only definite records from the Greater Antilles which have come to my attention are Santiago de las Vegas, Cuba; and Haiti. Both are by Banks under the name of *Pholcus tipuloides* Koch. It appears that no true *Pholcus*, a genus belonging to a different section of the subfamily, has been reported from the Greater Antilles, but the cosmopolitan *P. phalangoides* (Fuesslin) will undoubtedly be found. *Smeringopus* is a widespread tropical genus.

⁵ Since writing the above I have heard from Mr. Banks that he has seen it from Havana, Cuba. It is not included in the discussion at the end of this paper.

THERIDIIDÆ

The members of this large family spin irregular webs and certain of them are very common about human habitations.

Argyrodes is found throughout the tropics and subtropics. We took what Mr. Banks identified as *A. larratus* Keyserling in a narrow steep ravine near Baños San Vincente, Cuba, and an unidentified species, probably the same, in a similar ravine near Merciditas, a few kilometers farther north. This species is now considered to be a synonym of *cancellatus* (Hentz) and the range is Connecticut to †Alabama, Venezuela and St. Vincent. *A. nephilæ* Taczanowski is known from southeastern United States, Peru, Brazil, †Guiana, Haiti and Bermuda. We found it on both Mona and Desecheo. *A. trituberculatus* Becker has been recorded from †Mississippi and Haiti.

Rhomphæa is found throughout most of the world's tropics and subtropics. *R. paradoxa* (Taczanowski) was described from Guiana and has been reported from St. Vincent, but not elsewhere in the Antilles. Keyserling states that it is probably only a variety of *fictilium* (Hentz) which is the only known species in the United States and extends from New England to Florida.

Spintharus contains but two species, one confined to Brazil and one, *flavidus* Hentz, which was described from Alabama and is now known from all the States to Peru and from St. Vincent. It is a yellow, red and black creature usually found on the under side of the leaves of small bushes and should be looked for in the Greater Antilles.

Theridion is a large genus which is found throughout the world. Curiously enough, with the exception of certain cosmopolitan species, records from the Greater Antilles are almost lacking. We took *antiltanum* Simon, hitherto only known from St. Vincent, by beating branches in a sea-grape thicket at Dorodo, near San Juan, Porto Rico, and also in a narrow ravine in the mountains north of Viñales, Cuba. *T. frondeum* Hentz is found from Labrador (specimen in our collection) to Lower California and on St. Vincent. It will probably be found in the Greater Antilles. We took *fuesslyi* Simon, formerly known only from St. Vincent, by sweeping the tall grass and shrubs on the southwest coast of Desecheo. Among the wide ranging tropical and subtropical species are *rufipes* Lucas, *studiosum* Hentz, *tepidariorum* C. Koch, and *vituperabile* Petrunkevitch. We have the first two from the Bahamas but the only record for any of them from the Greater Antilles is that by Banks of *studiosum* Hentz from Haiti. It was described from South Carolina and Alabama and is known not only from "tropical and subtropical North

and South America" but also from Bermuda. Finally, *volatile* Keyserling is recorded from Florida, †Venezuela and (immature specimen) Culebra Island, Porto Rico.⁶

Theridula is found in the Mediterranean region, Africa, Madagascar, tropical and eastern Asia, Japan, Philippines and in America from Labrador (*opulenta* in our collection) to Peru and Brazil. Simon gives the distribution of *opulenta* Hentz as the Mediterranean region, western Africa and the Transvaal, Madagascar, Ceylon, the Antilles and North America. It was described from Georgia. There are a number of synonyms which extend its distribution to Peru and complicate matters. Banks reported it, under the name of *triangularis* Keyserling from Cayamas, Cuba, and from Haiti. He also reported *spharula* (Hentz), probably another synonym, from Haiti. He identified the specimens which we took in Cuba at Cabañas, Cerro de Cabras (near Piñar del Rio), Baños San Vincente, and Guane as *triangularis*, and others which we took at Cerro de Cabras as *quadripunctata* Keyserling. This latter is probably also a synonym. Apparently there are no other records for the Greater Antilles.

Latrodectus is found throughout most of the tropical and subtropical world, including Madagascar and Australia. The species tend to have bright red markings and "have been notorious in all ages and in all regions of the world where they occur on account of the reputed deadly nature of their bite" (Cambridge). *L. mactans* (Fabricius) extends outside even the subtropics, being found from New York to Tierra del Fuego. Cambridge (Proc. Zool. Soc. London, April, 1902, p. 253) points out that it is hardly separable from *tredecim-guttatus*, which is found in the Canaries, Madeira and the Mediterranean region. The only West Indian record is by Banks at Mayaguez, Porto Rico and Cockerell in Jamaica. We took it at Cabañas and Baños San Vincente in Cuba. *L. geometricus* C. Koch is found in Cape Verde Islands, Africa, Madagascar, India, Australia, Bermuda and tropical South America, the type locality being Colombia. The only West Indian records I have seen are Santiago de las Vegas and Havana, Cuba.

Petrunkévitch gives the distribution of *Teutana grossa* (C. Koch) as "Mexico, Guatemala, Costa Rica, West Indies, Brazil, Uruguay, Chile, Argentina, Is. Juan Fernandez, (Europe, Africa)." I can find no authority for the West Indies and believe that he mistranslated Simon's

⁶ Since writing the above I have heard from Mr. Banks that he has seen *Theridion interruptum* Banks and *T. rufipes* Lucas from Havana, Cuba. The former is known elsewhere only in Florida, but the latter is a cosmotropical species. They are not included in the discussion at the end of this paper.

"les îles de l'Atlantique," although there is no reason for not expecting it in the West Indies.

Lithyphantes is a cosmopolitan genus which has been recorded on the American mainland from Canada to Patagonia, but not from the Antilles. We took *septemmaculatus* Keyserling in Cuba in a mangrove swamp near Cabañas and in a flower garden at Baños San Vicente in the mountains. The localities given in the original description are stated as follows: "Herr Marx fing dieses Thier im Juli bei Denver in Columbia und im December bei Enterprise in Florida." Doubtless Denver, Colorado, was intended. It is also recorded from Curaçao.

Mysmena is known from France, northern Africa, Ceylon, Philippines and United States (two species, both in Florida, one of them being known also from the District of Columbia). We got several young specimens of the genus from the fallen leaves at the base of the cliffs at Baños San Vicente, near Viñales, Cuba.

Theridionexus cavernicolus Petrunkevitch is the only species in its genus and is known only from the Peru Cave in Jamaica. Although he places this creature among the Theridiidæ, Petrunkevitch says: "Its general appearance, the long front legs and the globose abdomen, and most of all the presence of a well developed tarsal comb, speak for its close relation to the family Theridiidæ. On the other hand, the structure of the mandibles, the shape of the cephalothorax, and especially the presence of a tibial apophysis in the male palpus, are characters which are found only in the Argiopidæ. It is, therefore, impossible to place the genus *Theridionexus* with sufficient reason in either of these families: it forms a new, intermediate group." From the standpoint of phylogeny, perhaps one might say it belongs to an old intermediate group, and if this be true its discovery, in a cave in the mountains of Jamaica has an added interest.

LINYPHIIDÆ

The distribution in America of this family is interesting. For the most part it is northern, but it has a number of representatives in southern South America and very few between. In addition to certain genera found only in Greenland or the extreme northern part of the hemisphere and others found only in southern Patagonia or Tierra del Fuego, there are others such as *Gonatium* and *Gongylidiellum* which are found at both extremes but not between. This discontinuous distribution may be due to faulty taxonomy or there may be natural causes for it. It is, however, not unknown in other organisms or even in other groups of spiders. This family is sometimes considered to be a subfamily of Argiopidæ.

Bathypantes is known from Europe, Asia, Australia and New Zealand, as well as from America. Of the forty American species, thirty-one are not recorded south of the United States, four are more southern but not known south of Guatemala, and four are from the extreme southern part of South America. The final one is the recently described *semicincla* Banks, collected by us in a flower garden at Baños San Vincente, near Viñales, Cuba.

Ceratinella is a palaearctic genus which has one species in this hemisphere. This species, *brunnea* Emerton, is found from Labrador (specimen in our collection) to New York. We also have a specimen of the genus, species undetermined, from the pine-palmetto plains south of Piñar del Rio, Cuba.

Ceratinopsis is an American genus with twenty-three species of which eleven are not recorded south of the United States (except, now, see *anglicana*); three from Mexico or Central America; and of the nine South American ones about half are confined to the southern part of that continent, three of them being known only from the region of Tierra del Fuego. We took *anglicana* (Hentz) by beating oak branches in a dense thicket at about 125 meters elevation on Cerro de Cabras, near Piñar del Rio, Cuba. We also took the genus, species undetermined, in a ravine at an elevation of about 300 meters near Baños San Vincente, Cuba. There are no other records for the genus in the West Indies.

Linyphia is another genus which extends from the northern to the southern extremes of this hemisphere, in fact it is nearly world wide in its distribution, but it is rather better developed in the tropics than some of its relatives. The only West Indian species is *coccinea* Hentz, which is found in †Florida and Haiti.

Microneta has a wide distribution, especially in temperate regions. In America there are twenty-one species confined to northern United States and Canada; one to Mexico; one (*varia* Simon) to St. Vincent; and one to Brazil. If the last two are correctly placed, the genus is likely to be found in the Greater Antilles.

ARGIOPIDÆ

This large family which includes the true orb-weavers is unsatisfactory material for a study of distribution because of the uncertain limits of some of the genera. Petrunkevitch and others have dodged the issue by putting eighteen of them in the Cohors *Araneus*, and I can only do likewise, putting, however, the probable generic name in parentheses. One of the subfamilies (*Linyphiinæ*) into which Simon divides the Argiopidæ has already been considered, treating it as a family.

TETRAGNATHINÆ

Cyatholipus is a genus erected by Simon to contain two of his species from southern Africa and one, *dentipes* Simon, from Jamaica. It is so distinct that Simon considers it to be the representative of a special group of the subfamily.

Tetragnatha is an almost cosmopolitan genus. The known distribution of *antillana* Simon is Mexico, Central America, Porto Rico (Lares), and St. Vincent. *T. elongata* Walckenaer may be found in the Greater Antilles as, although it is a species of Canada and United States, Walckenaer has recorded it from Guadeloupe. It occurs near streams and usually hangs its web partly, at least, over the water. *T. laboriosa* Hentz has been recorded from Alaska, much of the United States and Porto Rico (Utuado). Mr. Banks writes me that he has seen a specimen from Havana. *T. piscatoria* Simon has been reported only from St. Vincent but we found it in Porto Rico at an altitude of about 500 meters on El Duque and also near Arecibo. *T. vicina* Simon is recorded from †St. Vincent and Porto Rico (San Juan). Banks records the genus from Haiti on the basis of immature specimens and we have a number of such specimens from the edge of a mangrove swamp near Cabañas, Cuba. See also the discussion of Eugnatha.

Eugnatha is probably not more than a subgenus of *Tetragnatha* but, following Banks and Petrunkevitch, it will be separately considered. There is one species apparently confined to Mexico and one to northern United States. *E. pallescens* (F. Cambridge) is recorded from †New York, New Jersey, Florida, Texas, New Mexico, Mexico and Cuba (Santiago de las Vegas and Havana). *E. gracilis* Cambridge is recorded from Mexico, †Guatemala and Bayamon, Porto Rico. We found it at Naguaba, San Juan and Mayaguez in Porto Rico and at Baños San Vincente in Cuba.

Meta, as construed by Simon and others, is a fairly large and almost cosmopolitan genus. As is pointed out below, Mr. Banks considers *bigibbosa* (Keyserling) to be a *Leucauge* and he expressed his further opinion that *Meta* does not occur in the tropics of America at least.

Alcimosphenus has two species: *bifurcatus* Petrunkevitch from Jamaica; and *licinus* Simon. The latter is recorded from St. Vincent; Adjuntas, Porto Rico; Haiti and †Santo Domingo; Santiago de las Vegas, Cuba; and †Jamaica. We found it in Cuba at Cerro de Cabras and Baños San Vincente.

Leucauge, more widely known as *Argyroëpeira*, is a large genus which is generally distributed in the warmer parts of the world. *L. argyra*

(Walckenaer) ranges from California and Florida to Brazil and is recorded also from Cuba (Havana), Haiti, Porto Rico (Aguadilla, Arroyo, Lares and El Yunque), Vieques, †Guadeloupe and St. Vincent. We took it at nearly all stations from Guane to Guantanamo in Cuba, at Hope Gardens and Montego Bay in Jamaica, on Mona, and at Arecibo and San Juan in Porto Rico. *L. regnyi* (Simon) has been recorded only from St. Vincent, although it is possible, as suggested to me by Mr. Banks, that *Argyroëpeira bigibbosa* Keyserling, which Petrunkevitch questionably put in *Meta*, is a synonym. If so, its range includes also Colombia, Porto Rico (Aguadilla and El Yunque) and Haiti. In that case *bigibbosa* is the prior name. We took it in Porto Rico in the foothills of El Duque near Naguabo and at Arecibo, on Mona and Desecheo, and very commonly throughout Cuba. *L. venusta* (Walckenaer) is more generally known as *Argyroëpeira hortorum* (Hentz) Emerton. It is fairly common throughout the United States (Georgia being the type locality) and south to Colombia. Its recorded insular distribution is Bermuda, Bahamas, Cuba (Santiago de las Vegas) and St. Vincent. We did not take it in Cuba but did on Mona and in the mountains south of Arecibo, Porto Rico. As it is a very striking "green and silver-white spider, tinged with golden, and sometimes with orange-yellow or copper-red spots" and usually rests in a conspicuous web, it is not likely to be overlooked.

Dolichognatha is found in Ceylon, western Africa, and (the species given here) tropical and subtropical America. It is closely related to *Diphya* which has a somewhat similar distribution: South Africa, Madagascar, and Chile. *D. tuberculata* (Keyserling) has been found in †Florida, Mexico, Costa Rica, Venezuela and St. Vincent. It will probably be found in the Greater Antilles.

NEPHILINÆ

Nephila is found throughout much of the warmer parts of the world but seems to be rare in the West Indies. *clavipes* (Linnaeus) being the only species recorded, although it has gone under a number of names, of which *wilderi*, *wistariana* and *concolor*, all by McCook, should be mentioned. Its known range is from southern United States to Peru and Brazil, Bermuda, Bahamas, †Jamaica, Santo Domingo and Porto Rico (Aguadillo). We took an immature *Nephila* at Cabañas, Cuba, and as Mr. Banks has seen a specimen of *clavipes* from Havana our specimen doubtless belongs to this species. We have a number of adults from Mona.

ARGIOPINÆ

Argiope is found in the warmer parts of the world, less frequently in the temperate. Three (*aurantia* and the two mentioned here) of the eight American species are wide ranging but the others are more restricted. *A. argentata* (Fabricius) is said to be found from southern United States to Patagonia, including all the islands. Among the latter are St. Vincent, Martinique, Culebra, Porto Rico (San Juan, Utuado and Aguadilla), Santo Domingo and Isle of Pines. We also have it from several stations in Jamaica. *A. trifasciata* (Forsk.) is almost cosmopolitan. Combining the records of Banks (*fastuosa* Olivier) and our captures, it is safe to say that it is found throughout Cuba and Banks had it from San Juan, Porto Rico, but I know of no other definite records from the Antilles. We have a number of undetermined specimens of the genus from Mona, Desecheo and Porto Rico (San Juan and Arecibo) which may be one, or both, of these species.

Gea is known from West Africa, tropical Asia, East Indies, Polynesia, Australia and, by two species, America. One of these is reported only from Mexico. The other, *heptagon* (Hentz) has been found in †south-eastern United States as far north as the District of Columbia, in Guatemala, Brazil and Cuba (Havana). We took it in Cuba at Piñar del Rio and Baños San Vincente.

Cyrtophora is found throughout the tropical and subtropical world. It has three species in northern South America; one in California; and one, *sellata* Simon, in Santo Domingo.

Cyclosa has a world-wide distribution. *C. caroli* (Hentz) is found from southern United States (†Alabama) to Venezuela; also in St. Vincent and at Havana, Cuba. *C. oculata* (Walckenaer) was described from Europe (France and Italy) but Simon says it is probably of American origin and introduced to Europe where it is rare and localized. The American localities given by him are Venezuela and "Antilles." It would be interesting to know which of the Antilles are concerned and how abundant and widespread the species is in this hemisphere. The recorded distribution of *C. walckenaeri* (Cambridge) is California, Mexico to †Colombia, Brazil, Cuba (Santiago de las Vegas) and Haiti. We took it in Cuba also at Cerro de Cabras near Piñar del Rio.

Edricus is an American genus with a range from Mexico to Peru and Brazil. We took *crassicauda* (Keyserling) in the mountains about midway between Arecibo and Utuado, Porto Rico. This species is found on the mainland from Mexico to †Colombia.

Mangora has a wide distribution but has not been reported from Africa, Madagascar, the Pacific Islands or Australia. Neither has it

previously been reported from the West Indies although it is known to extend from northern United States to Brazil. We took a common United States species, *placida* (Hentz), in the Cerro de Cabras near Piñar del Rio, Cuba. This is not a species which would be likely to be carried by commerce, and although the United States Army operated to some extent in these hills it is not probable that this is a human introduction. If it were we would have expected to find the species nearer the regular lines of traffic. Alabama is the type locality.

Acacesia foliata (Hentz) is the only species in the genus as construed by Petrunkevitch. It is recorded from New England to Panama and from Haiti. It was described from Alabama.

Eustala is a fairly large American genus, chiefly found in Central America but ranging throughout most of the mainland south of Canada. *E. anastera* (Walckenaer) has many synonyms, the most common of which is *Epeira prompta*. It was described from Georgia and its distribution includes most of the United States and southward to Costa Rica and the Galapagos; Cuba (Cayamas and Havana according to Banks and Guane, Piñar del Rio, Baños San Vincente and Santiago in our collection), Haiti, Porto Rico (2800 feet altitude on El Yunque according to Banks and Arecibo in our collection) and St. Vincent. The variety, or separate species, *conchlea* (McCook) is known from †California, †Florida and Utuado, Porto Rico. The recorded distribution of *E. fuscovittata* (Keyserling) is Mexico to Paraguay, Guatemala being the type locality, Cuba, Porto Rico and St. Vincent. We found it in nearly all parts of Cuba and Porto Rico which we visited but not on Mona or Desecheo.

Drexelia is probably a synonym of *Larinia*, a genus found throughout most of the subtropical, and, more rarely, tropical world. As limited here (following McCook, Cambridge and Petrunkevitch) there are two species in America: one in Mexico, and one, *directa* (Hentz), recorded from †southeastern United States to Panama and at Havana, Cuba. We took it in several places on the plain south of Piñar del Rio, Cuba.

Cohors **Araneus**. As was stated above, this group includes a number of genera whose limits have not been clearly defined.

A. (Neoscona) arabesca (Walckenaer) is found on the mainland from Labrador to Mexico and also on Curaçao. We took it in western Cuba at Piñar del Rio and Guane by sweeping in meadow land. It was described from the Carolinas.

A. (Verrucosa) arenatus (Walckenaer) was described from Georgia and is known from New Jersey west to California and south to Panama. McCook says: "I have specimens collected by the late Mr. W. H. Gabb from San Domingo varying in but slight particulars from those above described."

A. (*Eriophora*) balaustinus McCook is recorded from †Florida to Lower California and Mexico; San Juan, Porto Rico; Haiti and Santo Domingo; Cayamas and Havana, Cuba; Jamaica; and Swan Island. The latter island, lying between Cuba or Jamaica and Central America, is a very interesting locality. It is to be regretted that we know so little of its fauna. We took this species on Mona and in a rotten banana trunk near Arecibo, Porto Rico.

A. (*Neoscona*) benjaminus (Walcenær). Labrador (in our collection) to Guiana and in Martinique. It is probably in the Greater Antilles.

A. (*Epeira*) bispinosus (Keyserling) is recorded from †California, Arizona, Panama and Haiti.

A. (*Singa*) crewii (Banks). †Haiti.

A. (*Singa*) cubana (Banks). The type locality is Havana, Cuba. We took it on the same island at Piñar del Rio and Baños San Vincente by sweeping the grass at the edge of water.

A. (*Neoscona*?) granadensis (Keyserling) is recorded from †Colombia and the Luquillo, Porto Rico. In giving the latter record, Banks remarks that it is close to *trivittata* Keyserling which is here considered to be a synonym of *arabesca*.

A. (*Epeira*) gundlachi (Banks) was described from a specimen taken by us on the sandy plain about 12 kilometers south of Piñar del Rio, Cuba.

A. (*Epeira*) incertus (Cambridge), described from Costa Rica, has hitherto been known only from Mexico and Central America. We got it in Cuba at Cabañas and Esperanza on the edge of mangrove swamps, in the mountains north of Viñales on oaks, and south of Piñar del Rio on the palmettoes of the dry sandy plains. A species so catholic in its ecological tastes is doubtless more widely distributed than these records show.

A. (*Metepeira*) labyrinthus (Hentz) is said to occur "from Labrador to Patagonia, including all the islands." The only definite Antillean records I have seen are Barbados; St. Vincent; Culebra and Vieques; Aguadilla, Porto Rico; and Havana, Cuba. We took it at Mayaguez, Porto Rico, and on Desecheo. Its type locality is North Carolina.

A. (*Verrucosa*) mexicanus (Lucas) of which *undecimvariolata* Cambridge is considered to be a synonym is known from Panama, Costa Rica, †Guatemala, Mexico and Santo Domingo.

A. (*Neoscona*) nauticus (L. Koch) was described from Africa. It is said to be found throughout the world's tropics and also in New Hampshire and Tennessee. Its only Antillean records are St. Vincent and Haiti.

A. (*Neoscona*) *neotheis* Petrunkevitch is a name proposed for *theisii* of Keyserling and McCook but not *theis* of Walckenær which is a Polynesian species. If this synonymy be followed, the known distribution is California, Mexico, Guatemala and probably the following Antillean localities,—Culebra; El Yunque, Bayamon, Aguadilla and Mayaguez, Porto Rico; and Haiti. In giving the Porto Rican records Banks says that “[*theisii*] is smaller and more slender than *E. oaxacensis* Keyserling, and I think different, although small specimens of the latter look much like large specimens of the former.” See the next species.

A. (*Neoscona*) *oaxacensis* (Keyserling) is, as is indicated above, confused with *neotheis*. Petrunkevitch gives its distribution as Pacific Coast of United States, †Mexico, Panama and St. Vincent. Banks recorded it from Santiago de las Vegas, Herradura and Havana in Cuba but made *theisii* Keyserling a synonym. Specimens taken by us at Cabañas and Piñar del Rio in Cuba, on Mona, and at Mayaguez, Arecibo, Manati, San Juan and Naguabo in Porto Rico were identified by Mr. Banks as this species.

A. (*Epeira*) *pegnia* (Walckenær) is recorded from Colombia, Costa Rica and most of the United States. Mr. Banks has written me that he has seen *Epeira globosa* Keyserling, here considered to be a synonym, from Havana, Cuba.

A. *perplexus* (Walckenær) was described as an *Epeira* in 1842 from Brazil and Santo Domingo but has, apparently, not been recognized since.

A. (*Epeira*) *pratensis* (Hentz) is recorded from most of the United States but not elsewhere. We took it near Baños San Vicente, Cuba, and Mr. Banks informs me that he has seen it from Havana.

A. (*Epeira*) *sericatus* Clerk apparently has a number of synonyms. Among them is *vulgaris* Hentz, the name which Mr. Banks gave to our specimens from Cabañas, Piñar del Rio and Guane, Cuba, as well as to those he had from Santiago de las Vegas and Havana in the same island. In all cases they were about houses and may have been introduced. The only other American records are from the continent north of Mexico. It is also found in †Europe.

A. (*Marxia*) *stellatus* Walckenær was described from southeastern United States and is found from Labrador (specimen in our collection) to Guatemala. We took it on the plain ten kilometers south of Piñar del Rio, Cuba, at the edge of a swampy area.

A. (*Wagneriana*) *tauricornis* (Cambridge) was described from a number of localities in Guatemala and Panama. It is recorded also from Colombia, Mexico, Louisiana, Alabama, Florida, Cuba (Santiago de las Vegas) and Haiti.

A. (Wagneriana) undecimtuberculatus (Keyserling) is known from †Colombia, Panama, Guatemala, Mexico, Florida, Cuba (Santiago de las Vegas) and Haiti.

A. (Eriophora) variolatus (Cambridge) is found in southern and western United States, Mexico, †Guatemala, Venezuela and St. Vincent. It is probably in the Greater Antilles also.

A. (Metazygia) wittfeldæ (McCook) is known from †Florida, Mexico, the Bahamas and Havana, Cuba. We took it at Mayaguez, Porto Rico, in a hotel.

Gasteracantha is widely distributed in the tropical and subtropical regions of the world. *G. cancriformis* (Linnæus) is found from North Carolina and California to Paraguay; the Bahamas: El Guama, Santiago de las Vegas and Havana, Cuba (according to Banks under the name of *hexacantha* Fabricius); Haiti and Jamaica. We have it from the Bahamas, Jamaica, Mona and Baños San Vicente in Cuba. *G. hilaris* Thorell is recorded from †St. Bartholomy, Porto Rico (Aguadillo and Adjuntas), and Haiti. In Porto Rico we found the under side of leaves of young coco palms at San Juan and also in the mountains south of Arecibo festooned with its webs. Banks has referred *G. canestrinii* Cambridge to this species, thus extending its range to Antigua and Dominica, but Petrunkevitch does not follow him in this. *G. sexserrata* (Walckenaer) is recorded from †Cayenne, Haiti and Porto Rico (Bayamon). I took it several years ago on Key Largo, Florida, so it is probably in Cuba also. *G. tetracantha* (Linnæus) is recorded from California (if *pallida* Koch be a synonym), Haiti, Culebra, St. Thomas, St. Vincent, Guadeloupe and three of the Grenadines. We can now add to this list Porto Rico (near Arecibo) and Desecheo.

Micrathena is the Acrosoma of authors. As now constituted it contains more than 125 species, all American, and the great majority tropical. *M. armata* (Olivier) is known only from †Hispaniola and Jamaica. *M. cubana* (Banks) is recorded only from †San Diego de los Baños and possibly Havana, Cuba. We took it in Cuba at Baños San Vicente. *M. flavomaculata* (Keyserling) is known only from Haiti; and *forcipata* (Thorell) only from Cuba. *M. horrida* (Taczanowski) is recorded from Mexico, Peru, †Guiana, Brazil and Jamaica; *obtuspinata* (Keyserling) from †Mexico to Brazil and also from Porto Rico. Finally, *rufopunctata* (Butler) and *sloanei* (Walckenaer) are known only from Jamaica. It is decidedly curious that there are no records of the genus in the Lesser Antilles.

Glyptocranium is strictly an American genus. The related Old World genera are found in Australia, Africa and southern Asia. It has two

species which are found only north of Mexico (one ranging even to Alaska), two in Mexico and one, *gastercanthoides* (Nicolet), in Brazil, †Chile and Jamaica.

Epecthinula minutissima Simon is the only species of its genus and is known only from Jamaica. The genus is related to *Epecthina*, which has but a single species, found only in Venezuela. According to Simon, there are three other genera belonging to the same group of the Argiopinae. One of these is found only in northern South America; one in South Africa and western Australia; and one in Algeria, New Caledonia and northern South America.

MIMETIDÆ

This is a small, for the most part tropical, family the members of which are usually found near or on the ground and make no definite web. None have heretofore been recorded from the West Indies.

Mimetus is found in the Mediterranean region, Africa, India, New Zealand and America. In the latter hemisphere there are nine species, of which two are recorded only from South America, five from Mexico and Central America, one from North Carolina. The remaining one, *interfector* Hentz, ranges over much of United States and we took it on the sandy plain south of Piñar del Rio, Cuba. The genus occurs also in Porto Rico, for we took an immature specimen of it near Arecibo.

THOMISIDÆ

These are called crab-spiders, not only on account of their shape but also because they usually walk sidewise or backward. They spin no snares but catch their prey either by pursuit or by lying in wait for it, being much favored with concealing colors. It is a large family the American members being chiefly found in or near the tropics although it ranges from Greenland to Patagonia.

MISUMENINÆ

Misumenops is a split, possibly unwarranted, from the cosmopolitan *Misumena*, to include a number of American species. *M. americanus* (Keyserling) is recorded from United States, Guatemala and St. Vincent. *M. asperatus* (Hentz) ranges from Canada to Costa Rica and is known also from Cuba, Haiti, Porto Rico (Bayamon and El Yunque) and St. Vincent. We found it very common throughout Cuba and took it also on Mona and at Mayaguez and San Juan, Porto Rico. *M. bellulus* (Banks) is recorded only from Florida but Mr. Banks has written me

that he has it from Havana, Cuba. *M. celer* (Hentz) probably includes *M. spinosa* Keyserling. Mr. Banks has recorded *spinosa* from Santiago de las Vegas and Cayamas, Cuba, and has named the specimens which we took at nearly all of our stopping places in that island from Guane to Guantanamo *spinosa*, while he named the specimens which we took at Mayaguez, Arecibo, Manati and Naguabo in Porto Rico *celer*. On the mainland, *celer* is found from Massachusetts to Mexico. The known distribution of *oblongus* (Keyserling) is from Massachusetts to Illinois and south to Georgia and New Mexico; also in Cuba (Santiago de las Vegas). *M. viridans* (Banks) is recorded only from Florida but Mr. Banks has it from Havana, Cuba. See also the next genus.

Misumessus echinatus Banks was described from material beaten from oak trees on Cerro de Cabras near Piñar del Rio, Cuba. According to the system followed here, it should probably be put under *Misumenops*.

STEPHANOPSISINÆ

Isaloides contains but two species: one from Mexico and one, *tous-saintii* Banks, from †Haiti and Cuba. It is closely related to and considered by Simon to be not more than a sub-genus of *Hedana*. He would also include the South American genera *Diaa* and *Erissus*. This adds interest to the distribution data, one section of the genus being found only in Hispaniola and South America while the other section is known only from Ceylon, southwestern Asia, Philippines, Malasia, the Tonga Islands, Australia and New Zealand.

Stephanopsis is confined to Madagascar, Malasia, Melanesia, Polynesia, Australia and America. In America there is one species in Panama, eight in South America (chiefly Chile) and one in Tortola of the Virgin Islands. Banks has recorded the genus from Santiago de las Vegas, Cuba. He states that he had two species, both represented only by immature specimens, and suggests that one of them is a young *pentagona* Keyserling. This species is now considered to belong to *Onoculus*. The species is known from Panama, Peru and Brazil, and as *Onoculus* is solely a South American genus the interest in the distribution of *Stephanopsis* is not lessened.

Tobias is an American genus, four species being confined to northern South America and one, *rugosus* (Taczanowski), being recorded from Brazil, †Guiana, Peru, Central America and Haiti.

PHILODROMINÆ

Tibellus is widely distributed in the temperate regions of the world, less so in the warmer regions. In America there is one species confined

to each of Mexico, Guiana and Paraguay while the fourth species, *oblongus* (Walckenær), occurs in †Europe, Asia, Alaska and most of United States. We took the latter species on the dry plain nine kilometers south of Piñar del Rio, Cuba.

CLUBIONIDÆ

The Clubionids are frequently confused with the Drassids and their habits are much the same. They make nests in rolled leaves, under stones, or in rubbish. The alphabetical arrangement of genera used by Petrunkevitch is especially confusing in this family as there are very distinct divisions which may be of family rank. The arrangement of Simon will be followed here.

SELENOPINÆ

Selenops is the only genus. It is found throughout most of the world's tropics. They are flat creatures which crawl under bark or stones whence they dart out for their prey. *S. aissus* Walckenær is known from Bahamas, Tortugas, Cuba (Cayamas and Santiago de las Vegas) and †Martinique. We found it hiding back of the boards of a house at Cabañas, Cuba. MacLeay in describing *S. celer* (MacLeay) said that it is common in Cuba. We took it north of Viñales, Cuba, on banana trees. It is recorded only from this island and Buen Ayre, off the coast of Venezuela. *S. insularis* Keyserling is known from †Porto Rico (San Juan, at least) and Haiti. We took it on Desecheo in a rotten log and also under fallen leaves in a sea-grape thicket.

SPARASSINÆ

Heteropoda is also found throughout most of the world's tropics. There are only four American species: three confined to South America and the cosmo-tropical *renatoria* (Linnæus). The known West Indian distribution is Jamaica, Cuba (apparently throughout), Haiti, Porto Rico (San Juan) and St. Lucia. It is frequently brought north in fruit.

Olios is likewise a cosmo-tropical genus. *O. antiguensis* (Keyserling) is known from Haiti, Porto Rico (Utuado), Culebra and †Antigua. *O. bicolor* Banks was described from specimens which we took on Desecheo, Mona, and at San Turce near San Juan, Porto Rico. *O. maculatus* (Blackwell) is reported from Brazil and the "Antilles."

Pseudosparianthis is an American genus with one species in Mexico, two in Brazil, one in St. Vincent, and one, *cubana* Banks, in Cuba (†Havana and †Santiago de las Vegas).

CLUBIONINÆ

Anyphæna in America is largely northern but it does extend even to Patagonia. It is found also in Japan, the mountains of India and the western Mediterranean region. We took immature specimens of it near Cabañas, Piñar del Rio and Guantanamo in Cuba. *A. perpusilla* Banks is known only from Santiago de las Vegas, Cuba. *A. striata* Becker was described from Mississippi and is elsewhere known only by Banks's record, under the genus *Aysha*, from Santiago de las Vegas, Cuba. He also records under the same generic name *A. velox* Becker from Havana, Cuba. It is known also from †Mississippi, Florida and the Bahamas. *A. gracilipes* Banks is known only from Haiti.

Aysha is a small tropical American genus closely related to the preceding one. Nine species are found in the region from Central America to Brazil; one is confined to the Galapagos Islands; two, *ferox* Simon and *ravida* Simon, are recorded only from Santo Domingo; and, finally, *tenuis* (L. Koch) is known from Cuba, †Haiti, Santo Domingo, Porto Rico (San Juan), Culebra and St. Vincent. We took *tenuis* on Desecheo and obtained immature specimens of the genus on Mona.

Chiracanthium inclusum (Hentz) was reported by Banks from Santiago de las Vegas, Cuba and Aguadilla, Porto Rico. We took it at Guane and at Guantanamo, Cuba, but not between these two places. We also took it in Porto Rico near Quebradillas, in the seed pods of *Crotolaria retusca* which had been eaten out by Lepidopterous (*Utetheisa*) larvæ, and near Dorodo. It has been found in St. Vincent, Haiti, throughout much of †United States and in Mexico. The genus is nearly world-wide in its range.

Clubiona is another cosmopolitan genus but it is more abundant in temperate than in tropical regions. In America it extends from Labrador to Patagonia. Its best South American development is in Chile. *C. maritima* L. Koch is reported from Santiago de las Vegas, Cuba, and †St. Thomas. *C. pallens* Hentz occurs on the Atlantic Coast from Massachusetts to †Alabama, and we found it in a weedy meadow on Cerro de Cabras, Piñar del Rio, Cuba.

Eutichurus is reported only from Central and South America except for *insulanus* Banks, which is in Cuba, Haiti and †Bermuda.

Oxysoma has ten species in South America. As they are chiefly in the southern and western part, it is interesting that the eleventh (*cubana* Banks, omitted in Petrunkevitch's catalogue) should be found in Cuba. It was described from one male from Havana and has not been recorded elsewhere.

Wulfila is an American offshoot of *Anyphæna*. It is known only from Mexico, Central America, Bahamas and West Indies. There is one species recorded only from St. Vincent. *W. immaculata* Banks was described from specimens collected by us at the edge of a mangrove swamp near Cabañas, Cuba; on the dry coastal plain of Mona; and at an altitude of about 500 meters on El Duque, near Naguabo, Porto Rico. *W. pretiosa* Banks was described from a specimen which we took in the Rio Seco woods on the San Carlos Estate near Guantanamo, Cuba. *W. parvula* Banks is confined to Haiti and *tenuissima* Simon to Jamaica.

CTENINÆ

Ctenus is a cosmo-tropical genus. America has a large number of species but apparently none of them live north of southern United States and the Bahamas. St. Vincent and St. Lucia each have a peculiar species; *haitiensis* Strand is known only from Haiti and *malvernensis* Petrunkevitch only from Jamaica. We have the latter from Montego Bay, Jamaica, and unidentified specimens of the genus from Cuba (Baños San Vicente, Cerro de Cabras and Guantanamo). Banks recorded an immature *Ctenus* which "looks very much like *Ct. hibernalis* Hentz" from Santiago de las Vegas, Cuba. This species is known from Alabama, New Mexico, Mexico and the island of Buen Ayre. He also recorded a female *Ctenus* (*Microctenus*) which appears to be new from a cave near Pueblo Viejo, Porto Rico.

Cupiennius is a South and Central American genus except for one species which comes as far north as Florida and *cubæ* Strand which is known only from Cuba.

It is interesting that, with the exception of widely distributed *Ctenus*, only one genus of this division (Cteneæ) of the Cteninæ is found outside of the middle portion of America. That is *Uliodon*, which is known only from Madagascar, New Zealand and Australia.

LIOCRANINÆ

Syrisca is found in Africa and America. There is one species in each of Colorado, Utah and Texas; two in South America, and two in the Greater Antilles. *S. insularis* (Lucas) is known only from Cuba and *keyserlingi* Simon (= *Teminius insularis*, Keyserling) only from †Haiti and Santiago de las Vegas, Cuba.

MICARIINÆ

Castaneira occurs in the western Mediterranean region, Africa, central Asia and America. It appears to be better developed in United States

and Mexico than it is farther south. The only West Indian record I have seen is a species confined to St. Vincent. We took a common United States species, *descripta* (Hentz), in a valley near Baños San Vincente, Cuba.

CORINNINÆ

Corinna is known from Africa, tropical Asia, Malasia and America. It is well developed in this hemisphere but, although there are eight species in St. Vincent which are not known elsewhere, only two species have been recorded from the remaining Antilles. *C. gracilipes* (Keyserling) is known from Havana, Cuba, and from †Haiti. *C. humilis* (Keyserling) has been recorded from Haiti, Porto Rico (Luquillo and Hacienda Esparanza) and †St. Kitts; Mr. Banks has written me that he has seen a specimen from Havana, Cuba; and we have a specimen from Mayaguez, Porto Rico, which is probably this species.

Trachelas occurs in the Mediterranean region, Africa, Madagascar, India, Malasia and America. In this hemisphere it appears to be best developed in Central America, but *bicolor* Keyserling is the only species recorded from the Greater Antilles. It is known only from Cayamas and Santiago de las Vegas, Cuba, and from †Haiti.

AGELENIDÆ

These are popularly called funnel-web spiders because many of the species spin flat webs which have a funnel-like passageway to their retreat. In America the family is best developed in the north and probably next best developed in the extreme south, being rather weak in the tropics except in the more mountainous regions.

Hahnia occurs in Europe and the Mediterranean region, the mountains of India, Sumatra, Japan and America. There are seven species not found south of the District of Columbia, one of them being known only from Greenland; two species are in Patagonia and Tierra del Fuego; and one, *ernsti* Simon, recorded only from St. Vincent, but taken by us in a rotten banana stump at about 500 meters elevation on El Duque, near Naguabo, Porto Rico.

Tegenaria is found throughout most of the cooler and, more rarely, in the warmer portions of the world. *T. domestica* (Clerk), better known as *derhami* (Scopoli), is said to inhabit the dwellings of man in all regions of the world, but I know of no definite record from the Antilles. *T. insularia* Walckenaer is known only from Cuba and has not been recorded since its description.

PISAUROIDÆ

The females of these, like those of the Lycosids, carry their egg sacs about with them. Some species also build a "nursery" for the newly hatched young, but construct no snare.

Thanatidius has one species in the Amazon region. The only other one known is *dubius* (Hentz), which has been reported from †North Carolina, Alabama, Florida and Cuba (Havana).

Thaumasia, as now constituted, is found only in the warmer parts of America. *T. marginella* (C. Koch) Simon is usually placed in *Dolomedes* and is recorded from Colombia, Brazil, Jamaica, Haiti, Vieques and possibly Porto Rico. We found it at Cabañas, Piñar del Rio and Baños San Vincente, Cuba. Mr. Banks has written me that he has seen it from Havana, Cuba. As he considers this species to be a *Dolomedes*, it may be that the immature specimens taken by us at Piñar del Rio and identified by him as *Dolomedes* belong to this species. As now construed, there are no records for *Dolomedes* in the Antilles.

LYCOSIDÆ

The relatively poor development in the Antilles of this fairly large family of "ground spiders" seems to accord with the distribution of Coleoptera (see Leng and Mutchler, 1914), among which the ground forms are more poorly represented than the arboreal ones. Bates, in his "Naturalist on the River Amazons," says: "It is vain to look for the Geodephaga, or carnivorous beetles, under stones, or anywhere, indeed, in open, sunny, places. The terrestrial forms of this interesting family, which abound in England and temperate countries generally, are scarce in the neighborhood of Pará—in fact, I met with only four or five species: on the other hand, the purely arboreal kinds were rather numerous. The contrary of this happens in northern latitudes, where the great majority of the species and genera are exclusively terrestrial. . . . The remarkable scarcity of ground beetles is doubtless attributable to the number of ants and Termites which people every inch of surface in all shady places and which would most likely destroy the larvæ of Coleoptera. These active creatures have the same functions as Coleoptera, and thus render their existence unnecessary. The large proportion of climbing forms of carnivorous beetles is an interesting fact, because it affords another instance of the arboreal character which animal forms tend to assume in equinoctial America, a circumstance which points to the slow adaptation of the Fauna to a forest-clad country, throughout an immense lapse of geological time." The last suggestion, in a modified form, seems

to be important. It may be that the fauna of "equinoctial America" is, to a large extent, a relic of past ages; that it arose in a forest-clad earth and has been driven before the more successful ground-inhabiting forms, not that it has been slowly developing from ground-inhabiting forms in the region in which it is now found.

Lycosa is a large genus of world-wide distribution. Several attempts have been made to split it up, with varying success. One of these puts *cinerea* (Fabricius) in the genus *Arctosa*. This species has been found in Europe, throughout United States, in Mexico and at El Guamá, Cuba. *L. atlantica* Marx was known only from Bermuda, but Mr. Banks writes that he has seen it from Havana, Cuba. *L. aussereri* (Keyserling) is known from †Colombia, Vieques and Culebra; *L. badia* (Keyserling) from Central America and Cuba; *L. fusca* (Keyserling) from Central America, Cuba (Havana, according to a letter from Mr. Banks) and Porto Rico (San Juan); *L. punctulata* Hentz, from United States east of the Rockies and, according to a letter from Mr. Banks, Havana, Cuba. *L. insularis* Lucas is known only from Cuba. We took it there at Guane, Piñar del Rio, Baños San Vincente, Cabañas and Guantanamo. Banks, who now considers it to be a *Pardosa*, recorded it from Santiago de las Vegas.

Pardosa is likewise of world-wide distribution. In America it is best developed in the north. There are a few species in South America, but unless *insularis* be included the only West Indian species is *portoricensis* Banks, which was described from San Juan, Porto Rico. We took it in a marsh at San Turce near its type locality.

These two genera, while much confused in the literature, are placed in different divisions of the family by Simon. Both are too generally distributed to be of a great deal of interest in a study of distribution.

OXYOPIDÆ

The members of this family run about the vegetation with great agility in chase of their prey. There are only eight genera, of which six occur in America. Of the remaining two, one is confined to Madagascar and one to India and Malasia. Two of the six American genera have not been reported from the Antilles; one of them has but two species and is confined to Brazil, and one has but one species, being confined to Cayenne, as far as is known.

Hamataliva has a wide tropical and subtropical range but in America there are only four species known: two in Brazil, one in Mexico and *grisea* Keyserling, which is reported from Lower California, southern United States, Cuba (Santiago de las Vegas) and Haiti.

Oxyopeidon is found in tropical east Africa, India, Indo-China and America. With us it seems to be confined to Mexico and Central America (six species) except for *rana* Simon, which has been known only from St. Vincent. We found this species fairly abundant on low vegetation on Mona.

Oxyopes is a nearly cosmo-tropical genus which extends into more temperate regions. In America it is best developed in Mexico and Central America, where there are numerous species. *O. pallidus* (C. Koch) was described from the West Indies, but the only definite locality record seems to be in Walckenaer's description of a male from Cuba. *O. salticus* Hentz is known from New York to †Alabama, Kansas, California and south to Bolivia, also in Bermuda, all the Greater Antilles and St. Vincent. It seems to be common throughout Cuba. We found it on Mona and near San Juan, Porto Rico. In Porto Rico it is also reported from El Yunque and Culebra.

Peucetia is also found throughout most of the tropical and subtropical regions of the world. *P. poeyi* (Lucas) is known only from Cuba, but *viridans* (Hentz) is distributed in America from †North Carolina to California and south to Costa Rica. It is recorded from Cuba (Santiago de las Vegas and Cayamas), Haiti and Jamaica. We have it from Kingston, Jamaica; Guane, Baños San Vincente, Oriente and Guantanamo in Cuba; and Mayaguez, Porto Rico. It has, apparently, not been found in the Lesser Antilles.

SALTICIDÆ

The "jumping spiders" make no snare but run about freely on the ground and on the vegetation in pursuit of their prey. The family is a large one and contains many species still to be described, while the taxonomy of the known forms is in a far from satisfactory shape. Our own West Indian collection was in the hands of Mr. Peckham and only partly worked up when he died. The following records, therefore, do not entirely cover the material which we have on hand.

Agobardus anormalis Keyserling is the only species in its genus. The type specimens are labeled U. S., but Petrunkevitch, following Peckham and Banks, states that it is probably from the West Indies.

Bythocrotus cephalotes (Simon) is not only the only species of the genus but the genus is the only one in Bythocrotea, one of Simon's divisions of the Salticidæ. It is not known outside of Haiti.

Compsodecta is an American genus with one species in Guatemala and two, namely, *albopalpis* (Peckham) and *grisea* (Peckham), in Jamaica. The genus belongs to Simon's group Pensacolea which con-

tains but two other genera, one of which is best represented in Brazil and Ecuador but extends to Mexico and the other is confined to tropical western Africa.

Corythalia is a fairly large tropical American genus. Two species, *major* (Simon) and *sellata* (Simon), are mentioned in Simon's "Histoire Naturelle des Araignees," II, pages 655 and 649, in such a way that Petrunkevitch was led to credit them to the West Indies, and, while this seems to me questionable, I can find no more definite reference. *C. metallica* (Peckham) is reported only from St. Vincent. Although it does not properly come within the scope of this paper, it is worth mentioning that we have it from Dominica. *C. elegantissima* (Simon) is known only from Santo Domingo, and *locuples* (Simon) from both parts of Hispaniola.

Stoidis is also an American genus. It contains but two species at present but specimens taken by us in Cuba were marked by Mr. Peckham as new species. *S. aurata* (Hentz) is known from †South Carolina and Florida. Mr. Banks has informed me that he has seen it from Havana, Cuba. *S. pygmaea* (Peckham) is reported only from St. Vincent but we took it in an epiphyte, *Tillandsia utriculata*, on Mona.

These two genera, *Corythalia* and *Stoidis*, are the only American representatives of Simon's Zenodorea. The other four genera are from Australia and the Pacific Islands.

The Cohors **Dendryphantes** of Petrunkevitch includes, in addition to some unplaced species which should probably be put in the genus *Dendryphantes*, the following genera: *Metaphidippus*, *Paraphidippus*, *Parnanus* and *Phidippus*. Although this cohort is in large part the genus *Dendryphantes* Koch as construed by Simon it is not very satisfactory for a study of distribution. The following list is arranged according to Petrunkevitch.

Dendryphantes armatus Banks (omitted by Petrunkevitch) was described from Santiago de las Vegas, Cuba, and has not been reported since.

D. (Phidippus) audax (Hentz) is known from Canada, throughout the United States and from Santiago de las Vegas, Cuba.

D. (Paraphidippus) aurantius (Lucas) is found from southern United States to Costa Rica and in Santo Domingo.

D. (Metaphidippus) capitatus (Hentz). Canada to Mexico and Santiago de las Vegas, Cuba (in Banks's list under name of *octavus* Hentz).

Dendryphantes mendicus (C. Koch) is credited to "West Indies" but no definite data is given.

D. (Phidippus) miniatus (Peckham). The known range is Virginia to Texas and at Santiago de las Vegas, Cuba.

D. (Phidippus) octopunctatus (Peckham) is reported only from Missouri but I took it in Dominica, the identification being by Peckham. It is, therefore, probably in the Greater Antilles.

D. (Metaphidippus) proximus Peckham was described from Cuba. Banks lists it from Santiago de las Vegas and we took it at Santiago de Cuba, Cristo, Zaza del Media, Cabañas, Cerro de Cabras and Baños San Vincente, Cuba. We have it also from Kingston, Jamaica.

D. (Metaphidippus) prudens Peckham is known only from Kingston, †Jamaica.

D. (Phidippus) regius (C. Koch) is known only from Cuba. Banks reports it at Santiago de las Vegas and we took it at Guane, a number of places in the vicinity of Piñar del Rio, north of Viñales (Baños San Vincente and Merciditas), Cabañas and Zaza del Media. All these localities are in central and western Cuba.

D. (Metaphidippus) taylori Peckham is known only from Jamaica.

Evophrys is found in Europe, Africa, Japan and America. There are about fifty American species, the genus ranging from New Hampshire to Patagonia. One species is found in St. Vincent, another in St. Thomas: it may, therefore, be found in the Greater Antilles but there do not seem to be any records as yet. The only other genus of *Evo-phrydeæ* is confined to Central America and northern South America.

Eustiromastix has seven species; three are confined to Brazil, one to Colombia, two to St. Vincent and *haytiensis* Banks to Haiti.

Hasarius adansonii (Adouin) is found throughout much of the world's tropics but I know of no West Indian records. It is the only American representative of the genus with the possible exception of *bellicosus* Peckham from Guatemala.

Hycitia is recorded only from Europe and United States. One of the three American species, *pikeli* Peckham, ranges from New England to New Mexico. We took it in Cuba at Cabañas, on the plains south of Piñar del Rio, and at Guane. Mr. Banks has written me that he has seen it from Havana.

Icius is given by Simon as being found in Europe, Africa and Asia but he does not give America. We have thirteen species, all found north of Mexico except one which is confined to Uruguay, one to Florida and the Bahamas, and *seperatus* Banks which is known only from Haiti.

Lyssomanes is a large American genus ranging from southern United States to Brazil. The *Lyssomanææ* includes seven genera, of which two are confined to America (the other one being found from Central America

to Guiana), two to Madagascar, one to India and Ceylon, one to the Philippines, and one is found in western Africa, Madagascar, the Seychelles, Ceylon, Burma and Indo-China. The group is evidently an ancient one. We have an undetermined specimen of *Lyssomanes* from Porto Rico. *L. antillanus* Peckham is known from both parts of Hispaniola and we have it from Jamaica (Lapland). *L. viridis* (Walckenaër), the most northern species of the genus, is known from southern United States, Central America, Haiti and (by letter from Mr. Banks) Havana, Cuba.

Marpissa occurs in Europe, Asia including Japan, and America. On the occidental mainland it ranges from northern United States to Brazil but the only Antillean record is *incerta* Koch from St. Thomas.

Menemerus bivittatus (Dufour) = *melanognatha* (Lucas) is almost cosmopolitan if the synonymy of Peckham and Petrunkevitch be accepted. Its only Antillean record, however, seems to be Santiago de las Vegas, Cuba. We have it from about plantation buildings at Cabañas, Cuba and also from Culebra.

Metacyrba is considered by Simon, but not by Petrunkevitch, to be a synonym of *Fuentes*. In any case it is solely American, and it belongs to a group, *Maviveæ*, which is known only from America. The only Antillean species is *pictipes* Banks from Haiti.

Myrmarachne is practically cosmopolitan. *M. melanocephalus* MacLeay is said by Lucas to be from Cuba and Petrunkevitch so records it without further comment, but the original description says it "is a native of Bengal and I present a figure of it, made by my friend Mr. C. Curtis, in order to show the relation which it bears to the American subgenus, called *Myrmecium* by Latreille." *M. parallelus* (Fabricius) has only the unsatisfactory record of "†Antilles."

Nilacantha cockerelli Peckham is the only species of its genus. It is found in Jamaica and Haiti. The Thiodinæ, to which it belongs, is an American group.

Peckhamia has but four species. It ranges, on the mainland, from Canada to Panama. A related genus, forming with it the group *Peckhamiæ*, is only known from Brazil. There are no records from the West Indies except for an immature specimen from Haiti, but Mr. Banks informs me that he has seen a specimen of the United States species, *P. picata* (Hentz), from Havana and we took an immature specimen of the genus at Cerro de Cabras near Piñar del Rio, Cuba.

Pellenes is found in Europe and the Mediterranean region, north-eastern Asia and America. In the latter region there are more than fifty species but it is not known south of Central America. There are

but two West Indian records: *banksi* Peckham and *translatus* Peckham, both confined to Jamaica. We took specimens of the genus which Mr. Peckham marked as new species at Cristo and Piñar del Rio, Cuba, and we also took *coronatus* (Hentz) at Piñar del Rio. This species ranges from New York to Mexico.

Plexippus is found throughout most of the world but especially in the warmer regions. *P. paykulli* (Adouin) is a cosmo-tropical species which has been recorded from Santiago de las Vegas and Havana, Cuba; Haiti; Lares, Adjuntas, San Juan and Arecibo, Porto Rico, and St. Vincent. We took it at Guane, Cuba.

Prostheclina Keyserling is considered by Simon to be synonymous with *Saitis*. This is probably correct but as there is some doubt they will be kept separate here except that, in giving the general distribution of *Saitis*, *Prostheclina* will be included. In America *Prostheclina* seems to be limited to the Greater Antilles. *P. parvula* Banks is known only from Cayamas, Cuba. *P. perplexides* Strand, *venatoria* Peckham, and *viaria* Peckham are known only from Jamaica (†Ipswich, †Port Antonio and †Moneague, respectively). *P. morgani* Peckham was described from Kingston, Jamaica, and *perplexa* Peckham from Mandeville, Jamaica. Both species are reported also from Haiti. *P. illustris* (C. Koch) was described from Porto Rico and has since been reported by Banks from an altitude of 2000 feet on El Yunque in that island. *P. signata* Banks is listed in the original description from Utuado and Aguadilla, Porto Rico; also from Culebra. He has since reported it from Haiti and we took it at San Turce and Dorodo, both near San Juan, and in the mountains south of Arecibo, Porto Rico, as well as on Desecheo.

Saitis, including *Prostheclina*, is known from southwestern Europe, western and southern Africa, India, Malasia, Polynesia, Australia and America. There are three species in South America; the others are from the Greater Antilles. With the exception of those mentioned under *Prostheclina*, all the known Antillean species are confined to Jamaica, namely, *annæ* Cockerell, †Kingston; *defloccatus* Peckham, †Kingston, and *inutilis* Peckham, no definite locality given.

Synemosyna is an American genus which, with *Simonella* from the American tropics, forms the group Synemosyneæ. Two species of *Synemosyna* are found in Brazil, one in St. Vincent, and the United States species, *formica* Hentz, is listed from Cayamas, Cuba.

Thiodina is an American genus which ranges farther north than the other members of the American group, Thiodineæ. *T. sylvana* (Hentz) is known from †South Carolina to Panama and, under the name of *retiaris* Hentz, from Cayamas, Cuba.

Wala is an American genus. *W. peckhami* (Cockerell) is known from †Jamaica and Haiti. We have it from Montego Bay, Jamaica, and Baños San Vicente, Cuba. *W. vernalis* (Peckham) has been reported from Santiago de las Vegas, Cuba; Jamaica; Haiti; San Juan and Aguadilla, Porto Rico; Vieques; †St. Vincent and Bermuda. We took it on Mona and Desecheo; and at Quebradillas, Manati, Dorodo, San Turce and Naguabo, Porto Rico. We also took undetermined specimens of the genus in the vicinity of Piñar del Rio, Viñales, Cabañas, Cristo and Guantanamo, all in Cuba.

Zygoballus and a Brazilian genus, together forming the group *Zygoballeæ*, are American. It ranges from Panama northward. The only record for the West Indies is *suavis* Peckham from Mandeville, Moneague and Kingston, †Jamaica. We have it from Montego Bay, Jamaica. We also have a specimen of the genus, marked by Peckham as a new species, from Cerro de Cabras, near Piñar del Rio, Cuba.

DISTRIBUTION OF FAMILIES

There are twenty-three families of Araneæ now known in the Greater Antilles. Five of these (Dictynidæ, Ecobiidæ, Oonopidæ, Dysderidæ and Mimetidæ) are added by this list. One family, Leptonetidæ, has three species, two genera, on St. Vincent, but it has not yet been found in the Greater Antilles, although it occurs on the mainland from California to Brazil. It is placed by Simon between the Sicariidæ and Oonopidæ. Its species are small, long-legged creatures for the most part cavernicolous, and should be looked for in the Greater Antilles. It is fairly widespread but is not yet known from southern Africa, Madagascar, Australia or the southern Pacific Islands.

There are eleven small families which are found on the mainland but have not, as yet, been reported from any of the Antilles. The Atypidæ (p. 77) and Hypochilidæ (p. 77) have already been mentioned. Zodariidæ is a large and widely distributed family which will probably be found in the West Indies. Senoculidæ are running spiders found only on the American mainland from Mexico throughout most of South America. The Archæidæ are interesting. There are three species of the type genus, *Archæa*, known from Baltic Amber but only one living species. This species is known only from Madagascar. The only other genus in the family is known by two species from Patagonia. The family Platoridæ has also an interesting distribution,—two genera in South America and one in China. The remaining six families (Zoropsidæ, Psecridæ, Eresidæ, Prodidomidæ, Zodariidæ and Hersiliidæ) have a wider distribution in the Old World.

Of the Antillean families, all are found from north of Mexico to South America except Palpimanidæ, which in America is known only from South America, St. Vincent and Cuba, and Caponiidæ, which in America is known only from Brazil to Mexico, St. Vincent, Hispaniola and Cuba (elsewhere only in South Africa). Table I summarizes the Antillean distribution of those families which are known from the Greater Antilles.

TABLE I.—*Antillean distribution of families of spiders*

	Lesser Antilles.	Culebra, Vieques.	Porto Rico.	Mona, Desecheo.	Hispaniola.	Cuba.	Jamaica.
Avicularidæ.....	×	×	×	:	×	×	×
Uloboridæ.....	×	:	×	×	×	×	:
Dictynidæ.....	:	:	:	:	:	×	:
Cecobiidæ.....	:	:	:	×	:	:	:
Filistatidæ.....	×	:	×	:	:	×	×
Sicariidæ.....	×	:	×	×	×	×	:
Oonopidæ.....	×	:	×	×	:	×	:
Dysderidæ.....	×	:	:	×	:	×	:
Caponiidæ.....	×	:	:	:	×	×	:
Drassidæ.....	×	:	:	:	×	×	:
Palpimanidæ.....	×	:	:	:	:	×	:
Pholcidæ.....	×	:	×	×	×	×	×
Theridiidæ.....	×	×	×	×	×	×	×
Linyphiidæ.....	×	:	:	:	×	×	:
Argiopidæ.....	×	×	×	×	×	×	×
Mimetidæ.....	:	:	×	:	:	×	:
Thomisidæ.....	×	:	×	×	×	×	:
Clubionidæ.....	×	×	×	×	×	×	×
Agelenidæ.....	×	:	×	:	:	×	:
Pisauridæ.....	:	×	×	:	×	×	×
Lycosidæ.....	×	×	×	:	:	×	:
Oxyopidæ.....	×	×	×	×	×	×	×
Salticidæ.....	×	×	×	×	×	×	×

It should be remembered that throughout this paper Lesser Antilles means little else than St. Vincent, since it is the only one of these islands which has been carefully studied. The need of work in Hispaniola is emphasized by the fact that one man collecting for only a few days on the small islands of Mona and Desecheo found representatives of twelve families, while but thirteen families are recorded from the large neighboring island of Hispaniola. It is strange that but nine families are known from Jamaica. This island has had the benefit of several workers, but poverty of its fauna is shown in other groups, so that this small number, while certainly not representing all the families to be found there, may be significant.

In view of the careful work done on St. Vincent, it is not likely that its number of families will be greatly increased. It lacks Dictynidæ, but this family is in the Greater Antillean list only by reason of a specimen from Guane, Cuba. It lacks Œcobiidæ, of which we found a species on Mona, but the family is otherwise unknown in the Antilles. Simon believes the species we found on Mona to be carried by commerce. It is curious that it should be on Mona, where there is almost no commerce, and not on St. Vincent, where there is a great deal. Mimetidæ are now known from Cuba and Porto Rico but not St. Vincent. They do not seem to be common even on the first mentioned islands as they had not previously been recorded and we have but one locality for each island. Finally, Pisauridæ, although not common, are recorded from all the Greater Antilles and from Vieques but from none of the Lesser. As they are, for the most part, rather large spiders, this is probably not due to defective collecting. It is probably one of those defects in distribution which are likely, when properly understood, to give us most valuable clues to the larger problems involved.

DISTRIBUTION OF GENERA

As a rule, family is somewhat too large a group to be of much value in a discussion of distribution and species is too small and uncertain, being not only no less human than other taxonomic groups but even more likely to be based on geographic range—the very thing we would like to use it to study. Accordingly genus seems the most favorable group to consider intensively.

The two Cohors of Petrunkevitch—*Araneus* and *Dendryphantes*—will be left out of consideration and also the following genera: *Ischnocolus*, *Mygale*, *Blechroscelis*, *Teutana*, *Agobardus*, *Pholcus* and *Hasarius*. The first two are not considered good genera; the next three are recorded from “West Indies” without further data; and the last two are said to be found throughout the tropical countries but no West Indian records are known.

LESSER ANTILLES

There are 108 genera of which 54 or just 50 per cent. are not known from the Greater Antilles. Seven, or 6.5 per cent., are peculiar to the Lesser Antilles. *Ischnothyreus* is not known elsewhere in America but is found in western Africa, Ceylon and the Philippines. Likewise, *Corinnomma* is known elsewhere only in Africa, eastern tropical Asia, Ceylon, Malasia, Papuasias, Philippines and Australia. In addition to the seven mentioned above there are 40 others which are not found in the Old

World. In other words, 43.5 per cent. are strictly American. Of these, one, *Alcimosphenus*, is known from Greater Antilles but not from the continent, 33 are known from South America, 21 are known from Central America, 14 are known from United States.

There are 59 genera which are known in America outside of the Lesser Antilles and are also known from the Old World. One of these, *Drymusa*, is known only from St. Vincent and Mona in the New World. In the Old World it is known only from Cape of Good Hope, one species being found in each hemisphere. Of the other 58, 56 (17) are known from South America, 44 (6) are known from Central America, 41 (4) are known from United States. Leaving out of account cosmopolitan or at least cosmotropical genera and those which are distributed pretty generally throughout the American-mainland, we have the numbers shown in parentheses. Let us now examine the distribution of these more in detail.

One of them, *Theonæ*, has one species in St. Vincent, one in Missouri, and the genus is represented also in France and Sumatra. *Hahnia* has several species from Virginia and Wyoming northward to Greenland, two in Patagonia and Terra del Fuego and one in St. Vincent and Porto Rico. It is unknown from the middle of the western mainland. In the eastern hemisphere it has been found in Europe, in the mountains of India, in Japan and Sumatra. *Bolostromus* is found in Alabama (one species), northwestern South America (four species), St. Vincent (one species) and southwestern Africa. *Oxyopeidon* has six species in Central America and Mexico, one of them reaching to Arizona, one species in St. Vincent and Mona, and in the Old World it is found in tropical east Africa, India and Indo-China.

One genus found in Central America has just been considered. The remaining five are found in both Central and South America but are not known from United States. One, *Beata*, is known only from this section of tropical American mainland, St. Thomas, St. Vincent and Africa. The details of the distribution of *Miagrammopes*, *Dysderina*, *Artema* and *Stephanopsis* may be had by consulting the taxonomic part of this paper. One is found in the Mediterranean region, three in Africa, three in Madagascar, two in continental Asia, one in the Philippines, two in Malasia, one in Melanesia, two in Polynesia and two in Australia.

Seven of the genera under discussion which are found in South America have been mentioned. The following ten are not known from the American mainland north of Panama and, with the exception of *Opopæa*, which we found on Desecheo, not even from any of the Antilles except St. Vincent: *Accola*, *Theotima*, *Oonops*, *Opopæa*, *Janulus*, *Episinopsis*, *Dyschiriognatha*, *Ogulnius*, *Anapis*, *Caloctenus*. One is found in Europe,

five in Africa, one in eastern Asia, two in Malay peninsula (one not being known elsewhere in the Old World), four in Ceylon (one not being known elsewhere in the Old World), one in New Caledonia, one in Japan, three in the Philippines (two not being known elsewhere in the Old World), two in Malasia and one in Australia.

I believe it is impossible to explain these distributions by accidental dispersal in relatively recent times through wind or otherwise or by any recent system of land bridges.

Taking into account all the genera found in the Lesser Antilles, we find that 22 (20.4 per cent. of the total) are practically world-wide in their distribution. This leaves 39 genera which have a more or less restricted range in the eastern hemisphere. Of these, 7 (18.0 per cent.) are found in central or northern Europe, 10 (25.6 per cent.) in the Mediterranean region, 23 (59.0 per cent.) in Africa, 5 (12.8 per cent.) in Madagascar, 20 (51.3 per cent.) in continental Asia, 10 (25.6 per cent.) in Ceylon, 8 (20.5 per cent.) in Japan, 8 (20.5 per cent.) in Philippines, 12 (30.8 per cent.) in Malasia, 5 (12.8 per cent.) in the smaller Pacific Islands, and 8 (20.5 per cent.) in Australia.

The American distribution outside of the Lesser Antilles of Lesser Antillean genera is shown in Table II. The study of this table had better be deferred until after the Greater Antilles have been considered.

TABLE II.—*American distribution of Lesser Antillean genera of spiders*¹

	Not on main- land	S. A. only	C. A. only	U. S. only	S. A. C. A.	C. A. U. S.	S. A. U. S.	S. A. C. A. U. S.	Total
Not in other Antilles.....	9	19	1	1	6	3	1	14	54
P. R. only.....	1	1	2	1	1	1	7
Hisp. only.....	..	1	1	2
Cuba only.....	..	3	..	1	2	1	..	3	10
Jam. only.....	1	1
P. R., Hisp.....	1	1
P. R., Cuba.....	1	3	4
Hisp., Cuba.....	1	3	4
Hisp., Jam.....	1	..	1
P. R., Hisp., Cuba.....	3	9	12
P. R., Cuba, Jam.....	2	2
Hisp., Cuba, Jam.	1	1	2
P. R., Hisp., Cuba, Jam....	..	1	1	..	1	5	8
Total.....	11	25	2	3	16	5	3	43	108

¹ Columns refer to the mainland and rows to the Antilles. "C. A." includes Mexico, and "U. S." includes everything north of Mexico.

PORTO RICO

Politically Porto Rico includes Culebra, Vieques, Desecheo and Mona. In Table II and in what follows these islands are included when Porto Rico is mentioned unless the context clearly implies a distinction. It seems that the only error this might cause would be to make the conclusion concerning the cosmopolitan character of the Porto Rican fauna less clear cut than it would be if we considered only the main island.

There are 51 genera known from the Porto Rican islands of which only 5 or 9.8 per cent. are not known from the other Antilles. It is interesting that four (*Stichoplastus*, *Æcobius*, *Mecolæsthus* and *Edricus*) of these five are added to the fauna by this list, while the other one (*Pardosa*) is credited as peculiar in the Antilles merely because a dubious taxonomic shift has taken a Cuban species out of the genus. No known genera are peculiar to the Porto Rican islands. All of these five genera are known elsewhere in America; one being found elsewhere only in South America; two only from South America to Mexico; one from Brazil to Massachusetts, in Azores, Canaries, Mediterranean region, Arabia, Japan and New Caledonia; and the fifth is practically cosmopolitan.

Unfortunately the standing of *Prostheclina* is in considerable doubt. As Simon considers it in part a synonym of *Saitis* it would be difficult to determine its Old World distribution. For details see page 107. It will be omitted from further discussion. As it occurs in the other Antilles, whether it be a synonym of *Saitis* or not, this omission does not affect the statements of the preceding paragraph.

Of the 50 remaining genera, 15 (30 per cent.) are restricted to America (including *Wala*, which is found in Bermuda). All of these are known from the continent, being distributed as follows: 12 are known from South America, 12 are known from Central America, 9 are known from United States.

Of the 35 genera found also in the Old World, only one, *Drymusa*, is not known from the American mainland. As has been stated its distribution is Mona, St. Vincent and Cape of Good Hope. Of the remaining 34, 33 (5) are known from South America, 32 (4) are known from Central America, 28 (2) are known from United States.

Leaving out, as was done in considering the Lesser Antilles, the rather generally distributed genera, we have the numbers shown in parentheses. They refer to *Miagrammopes*, *Dysderina*, *Opopæa*, *Artema*, *Hahnina*, and *Oxyopeidon*. The details of their distribution may be had by reference to the taxonomic part of this paper. All are found in the Lesser Antilles and only one (*Miagrammopes*) elsewhere in the Antilles.

Taking into account all the genera except *Prostheclina* known from the Porto Rican islands, we find that 22 (44 per cent. of the total) are practically world wide in their distribution. This leaves 13 genera which have a more or less restricted range in the eastern hemisphere. Of these, 1 (7.7 per cent.) is found in central Europe, 6 (46.2 per cent.) in the Mediterranean region, 11 (84.6 per cent.) in Africa, 3 (23.1 per cent.) in Madagascar, 9 (69.2 per cent.) in continental Asia, 1 (7.7 per cent.) in Ceylon, 3 (23.1 per cent.) in Japan, 3 (23.1 per cent.) in Philip-pines, 4 (30.8 per cent.) in Malasia, 2 (15.4 per cent.) in the smaller Pacific islands and 5 (38.5 per cent.) in Australia and New Zealand.

The American distribution outside of Porto Rico of Porto Rican genera is shown in Table III. It is worth noting in passing that of the

TABLE III.—*American distribution of Porto Rican genera of spiders*^{*}

	Not on main- land	S. A. only	C. A. only	U. S. only	S. A. C. A.	C. A. U. S.	S. A. U. S.	S. A. C. A. U. S.	Total
Not in other An- tilles.....	..	1	2	2	5
Lesser only.....	1	1	2	1	1	1	7
Hisp. only.....	..	1	1	2
Cuba only.....	1	..	2	3
Less., Hisp.....	1	1
Less., Cuba.....	1	3	4
Cuba, Jam.....	1	1
Less., Hisp., Cuba	3	9	12
Less., Cuba, Jam.	2	2
Hisp., Cuba, Jam.	5	5
Lesser, Hisp., Cuba, Jam.....	1	..	1	6	8
Total.....	1	3	1	1	8	2	1	33	50

50 genera considered, 34 are in the Lesser Antilles and 38 in the Greater. This would show a slightly greater affinity of the Porto Rican fauna with the islands to the west. However, many of these are widely distributed genera. It was seen above that all of the five genera having more or less restricted range and found also in the Old World are found in the Lesser Antilles and only one in the islands to the west. Adding *Phormictopus*, *Eugnatha*, *Wulfila*, *Aysha*, and *Stoidis*—the only strictly American genera found in Porto Rico which are not wide-ranging on the mainland—we find 8 in the Lesser Antilles and 6 in the islands to the west. It must be concluded that, as far as genera of spiders are con-

^{*} Columns refer to the mainland and rows to the Antilles. "C. A." includes Mexico, and "U. S." everything north of Mexico.

cerned, the Porto Rican fauna is as closely related to the Lesser Antillean as it is to that of the other Greater Antilles. This conclusion is strengthened by remembering that St. Vincent, an island well down in the string of Lesser Antilles, furnished almost all the data for that group of islands.

HISPANIOLA

Although some of the records for this island are credited to the Haitian portion of it through the unfortunate use of "Haiti" for the whole island, nevertheless most of them really came from Haiti, especially near Port au Prince, being those of Banks's list. It seems best to consider the island as a whole until we know more about the differences between the parts.

There are only 52 genera known from Hispaniola. This, clearly, is but a small part of its fauna, and since the more interesting genera, those of restricted range, are probably most abundant in the almost totally unstudied mountains, it is possibly not a fair sample. However, 9 genera, or 17.3 per cent., are not known elsewhere in the Antilles and 2 (*Scopelobates* and *Bythocrotus*), or 3.8 per cent., are peculiar to the island. *Trichopelma* is known elsewhere only from South America; *Tobias* only from Central America and northern South America; *Acacesia* only from southern United States to Panama (a single species throughout); *Metacyrba*, the same distribution except that it is also found in Buen Ayre, off the northern coast of South America; *Icius*, especially in United States (as far as American records go), Mexico, Uruguay, Europe, Africa and Asia; *Linyphia* and *Cyrtophora*, practically cosmopolitan but not recorded from the other Antilles.

Again leaving out *Prostheclina*, we find 24, or 47.1 per cent., of the remaining 51 are strictly American (including *Wala* and *Eutichurus*, which are known from Bermuda). Of these *Alcimosphenus* is known from St. Vincent, Cuba and Jamaica, and *Nilacantha* from Jamaica, but neither from the continent. These, with the two peculiar genera, leave 20 which are distributed as follows: 16 are known from South America, 17 are known from Central America, 11 are known from United States.

There are 27 Hispaniolan genera known elsewhere in America and also in the Old World. All are found in continental America and as follows: 27 (2) are known from South America, 25 (1) are known from Central America, 24 (1) are known from United States.

As before, the numbers in parentheses refer to genera of more restricted range. As a matter of fact only two are concerned: *Miagrammopes*, known from all the Greater Antilles except Jamaica, from St. Vincent, Brazil to Mexico, Africa, Madagascar, southern Asia and Australia; and

Syrisca, known from Cuba, southwestern United States, Brazil, Paraguay and Africa.

Considering all Hispaniolan genera except *Prostheclina*, 21 or 41.2 per cent. are almost world wide in their distribution. This leaves six (*Miagrammopes*, *Anyphæna*, *Syrisca*, *Trachelas*, *Corinna* and *Icius*) to be considered. Of these 1 (16.7 per cent.) is found in Europe, 2 (33.3 per cent.) in the Mediterranean region, 5 (83.3 per cent.) in Africa, 2 (33.3 per cent.) in Madagascar, 5 (83.3 per cent.) in continental Asia, 1 (16.7 per cent.) in Japan, 2 (33.3 per cent.) in Malasia and 1 (16.7 per cent.) in Australia.

The American distribution of Hispaniolan genera outside Hispaniola is shown in Table IV.

TABLE IV.—American distribution of Hispaniolan genera of spiders⁹

	Not on main- land	S. A. only	C. A. only	U. S. only	S. A. C. A.	C. A. U. S.	S. A. U. S.	S. A. C. A. U. S.	Total
Not in other An- tilles.....	2	1	1	1	1	3	9
Lesser only....	..	1	1	2
P. R. only.....	..	1	1	2
Cuba only.....	1	..	1	..	1	1	4
Jam. only.....	1	1
Less., P. R.	1	1
Less., Cuba.....	1	3	4
Less., Jam.....	1	1
Less., P. R., Cuba.	3	9	12
Less., Cuba, Jam.	1	1	2
P. R., Cuba, Jam.....	1	5	6
Less., P. R., Cuba, Jam.....	1	..	1	6	8
Total.....	5	3	2	0	8	2	2	30	52

CUBA

There are 82 genera recorded if *Misumessus echinatus* Banks be put under *Misumenops* and *Dolomedes* (see *Thaumasia*) be omitted. Of these, 24, or 29.3 per cent., are not known from the other Antilles, but only one (*Hapalopinus*), or 1.2 per cent., is peculiar to Cuba. Of the remaining 23, all are found in continental America. *Oxysoma* is confined to South America except for a single Cuban species. *Eilica* and *Thanatidius* are American genera and have but two species each on the main-

⁹ Columns refer to the mainland and rows to the Antilles. "C. A." includes Mexico, and "U. S." everything north of Mexico.

land, and in both cases one is in southeastern United States and the other in Brazil, but the Cuban species of *Eilica* is distinct, while that of *Thanatidius* is common to Cuba and United States. *Drexelia* is found throughout most of the world's tropics and subtropics, including Central America and United States, but has not been reported from South America or any of the Antilles except Cuba, while *Peckhamia* is known only from Panama northward on the American mainland and in Cuba. *Callilepis*, *Mysmena*, *Ceratinella* and *Hycia* are known in America only from Cuba and the mainland north of Mexico, but they are all found in Europe and elsewhere in the northern hemisphere. The other 14 are all widely distributed in America; *Eurypelma*, *Ceratinopsis*, *Cupiennius* and *Thiodina* being strictly American; *Smeringopus*, *Lithyphantes*, *Tibellus*, *Tegenaria* and *Myrmarachne* being at least cosmotropical; *Dictyna* occurring in Europe and Asia, including Japan and the Philippines; *Theridula*, in the Mediterranean region, Africa, Madagascar, tropical and eastern Asia, Japan and the Philippines; *Bathypantes*, in Europe, Asia, New Zealand and Australia; *Gea*, in western Africa, tropical Asia, the East Indies, Polynesia and Australia; and *Mangora*, in the Atlantic islands, Europe, Asia and Ceylon.

Prostheclina is troublesome, as before, and will be omitted. Including *Eutichurus* and *Wala*, which are found in Bermuda, 31, or 38.3 per cent., are restricted to America. With the exception of *Hapalopinus*, which is confined to Cuba, and *Alcimosphenus*, which is found in Jamaica, Hispaniola and the Lesser Antilles, all these are found on the mainland and are distributed as follows: 22 are known from South America, 20 are known from Central America, 18 are known from United States.

All of the 50 Cuban genera which are found in the Old World are also found on the American mainland. They are distributed as follows: 44 (3) are known from South America, 45 (3) are known from Central America, 46 (6) are known from United States.

As before, the numbers in parentheses refer to genera having a more or less restricted range. *Miagrammopes* is found from Brazil to Mexico, in St. Vincent and all the Greater Antilles except Jamaica, in Africa, Madagascar, southern Asia and Australia. *Callilepis* is widely distributed in the Old World but is confined to Cuba and north of Mexico in America. *Mysmena* is found in Cuba, southeastern United States, France, northern Africa, Ceylon and the Philippines. *Ceratinella* is known from Cuba, northeastern United States to Labrador and northern Eurasia. *Stephanopsis* ranges from Patagonia to Panama, in Tortola (Lesser Antilles), Cuba, Madagascar, Malasia, Melanesia, Polynesia and Australia. *Syrisca* is recorded from Brazil, Paraguay, southwestern United States, His-

paniola, Cuba and Africa. *Hycia* is in Cuba, most of the United States and Europe. *Pelienes* occurs in Cuba; Jamaica, Central America and northward, Europe, Mediterranean region and northeastern Asia.

Taking into account all the Cuban genera, we find that 29 (35.8 per cent. of the total) are practically world wide in their distribution. Of the remaining 21 which have a more or less restricted range in the Old World, 7 (33.3 per cent.) are found in central and northern Europe; 9 (42.9 per cent.) in the Mediterranean region; 13 (61.9 per cent.) in Africa; 5 (23.8 per cent.) in Madagascar; 15 (71.4 per cent.) in continental Asia; 2 (9.5 per cent.) in Ceylon; 4 (19.0 per cent.) in Japan; 4 (19.0 per cent.) in the Philippines; 4 (19.0 per cent.) in Malasia; 3 (14.3 per cent.) in the smaller Pacific islands and 8 (38.1 per cent.) in Australia and New Zealand.

The American distribution of Cuban genera is shown in Table V.

TABLE V.—American distribution of Cuban genera of spiders¹⁰

	Not on main- land	S. A. only	C. A. only	U. S. only	S. A. C. A.	C. A. U. S.	S. A. U. S.	S. A. C. A. U. S.	Total
Not in other An- tilles.....	1	1	..	4	..	2	2	14	24
Lesser only.....	..	3	..	1	2	..	1	3	10
P. R. only.....	1	..	2	3
Hisp. only.....	1	..	1	..	1	1	4
Jam. only.....	2	2
Less., P. R.....	1	3	4
Less., Hisp.....	1	3	4
P. R., Jam.....	1	1
Less., P. R., Hisp.	3	9	12
Less., P. R., Jam.	2	2
Less., Hisp., Jam.	1	1	2
P. R., Hisp., Jam.	5	5
Less., P. R., Hisp., Jam.....	1	..	1	6	8
Total.....	2	4	2	6	9	5	4	49	81

JAMAICA

Only 31 genera of spiders are known from Jamaica, including *Prostheclina*. Of these 7, or 22.6 per cent., are not found in the other Antilles. The question as to whether *Prostheclina* of Keyserling should be treated as a synonym of *Saitis* of Simon has been mentioned several times and *Prostheclina* has been omitted from the discussions when world-wide

¹⁰ Columns refer to the mainland and rows to the Antilles. "C. A." includes Mexico, and "U. S." everything north of Mexico.

distribution was concerned. In Jamaica we are troubled by the fact that three species of *Saitis* are recorded. There are three other species in South America and the genus in the broad sense is known from southwestern Europe, western and southern Africa, India, Malasia, Polynesia and Australia. If we include the records for *Prostheclina* with *Saitis* the result will be to decrease the apparent distinctness of Jamaica from the other Antilles, but as it is still quite distinct this would probably be the fairest course.

We then have 30 genera credited to Jamaica of which 6, or 20 per cent., are not known from the other Antilles. Of these 3, or 10 per cent., are not known elsewhere in America. *Theridionexus* and *Epecthinula* are confined to Jamaica and *Cyatholipus* has been found elsewhere only in South Africa. Fourteen genera (43.3 per cent.) are strictly American; 10, or 33.3 per cent., are practically cosmopolitan or cosmotropical. In addition to these and *Saitis* and *Cyatholipus*, which have just been mentioned, *Pachylomerus* is known from Jamaica, St. Vincent, Brazil (?), Venezuela to Maryland, the Mediterranean region and Japan. *Ischnothele* is found in Jamaica, South America to Mexico, Bahamas and either it or a closely related genus, which we will consider as it, in eastern Africa, Madagascar and India. *Filistata* is known from South America, including the Galapagos, to California and southeastern United States, Bermuda and the Atlantic islands, Mediterranean region, Africa, central Asia, Philippines and Australia. *Pellenes* is reported from Jamaica, Cuba, Central America to Canada, Europe, Mediterranean region and northeastern Asia. The numbers are so few that the reader can easily analyze the distributions from the data just given.

Of the 10 American genera which have been found on the mainland, 6 are known from South America, 10 are known from Central America and Mexico, 7 are known from United States.

The American distribution of Jamaican genera is shown in Table VI.

TABLE VI.—American distribution of Jamaican genera of spiders¹¹

	Not on main- land	S. A. only	C. A. only	U. S. only	S. A. C. A.	C. A. U. S.	S. A. U. S.	S. A. C. A. U. S.	Total
Not in other An- tilles.....	3	..	1	..	1	1	6
Lesser only.....	1	1
Hisp. only.....	1	1
Cuba only.....	2	2
Less., Hisp.....	1	1
P. R., Cuba.....	1	1
Less., P. R., Cuba	2	2
Less., Hisp., Cuba	1	1	2
P. R., Hisp., Cuba	..	1	5	6
Less., P. R., Hisp., Cuba.....	1	..	1	6	8
Total.....	5	1	2	0	3	3	0	16	30

GREATER ANTILLES

Omitting the two cohorts and the seven doubtful genera mentioned on page 000; also considering that *Misumessus echinatus* is a *Misumenops*, that the Antillean records for *Prostheclina* in Petrunkevitch's Catalogue should be credited to *Saitis* and that *Dolomedes* has not been recorded from Cuba, there are 11½ genera left, of which 63, or 53.8 per cent., are not known from the Lesser Antilles. Six, or 5.1 per cent., are peculiar to the Greater Antilles. They are *Hapalopinus* in Cuba, *Scopelobates* in Hispaniola, *Theridionerus* and *Epecthinula* in Jamaica, *Bythocrotus* in Hispaniola and *Nilacantha* in Hispaniola and Jamaica. *Cyatholipus* is not known in America outside of Jamaica but occurs in South Africa. In addition to the six mentioned above there are forty-four others which are not found in the Old World. In other words, 42.7 per cent. are strictly American. One of these, *Alcimosphenus*, is also known from the Lesser Antilles (St. Vincent) but not from the mainland: 33 are known from South America, 30 are known from Central America and Mexico, 24 are known from United States.

There are 66 genera which are known in America outside of the Greater Antilles and are also known from the Old World. One of these, *Drymusa*, is known only from Mona, St. Vincent and Cape of Good Hope. Of the other 65, 58 (9) are known from South America, 56 (7) are

¹¹ Columns refer to the mainland and rows to the Antilles. "C. A." includes Mexico, and "U. S." everything north of Mexico.

known from Central America and Mexico, 55 (7) are known from United States.

As before, the numbers in parentheses refer to genera of more or less restricted distribution. *Mysmena*, *Ceratinella* and *Hycia* are Holarctic genera which are for the first time in West Indian list and now only by reason of being found in Cuba. The others (*Ischnothele*, *Miagrammopes*, *Dysderina*, *Opopaea*, *Artema*, *Stephanopsis*, *Syrisca*, *Hahnia*, *Oryopeidon*, *Pellenes* and *Saitis*) are considered rather fully in the discussions concerning the individual islands and also in the taxonomic part of this paper.

Of the 117 genera in the Greater Antilles, 34 (29.1 per cent. of the total) are practically world wide in their distribution. This leaves 33 genera which have a more or less restricted range in the eastern hemisphere. Of these 10 (30.3 per cent.) are found in central or northern Europe; 13 (39.4 per cent.) in the Mediterranean region: 22 (66.7 per cent.) in Africa; 7 (21.2 per cent.) in Madagascar: 23 (69.7 per cent.) in continental Asia; 3 (9.1 per cent.) in Ceylon: 7 (21.2 per cent.) in Japan; 6 (18.2 per cent.) in the Philippines: 8 (24.2 per cent.) in Malasia: 5 (15.2 per cent.) in the smaller Pacific islands and 9 (27.3 per cent.) in Australia and New Zealand.

The American distribution of genera found in the Greater Antilles is shown in Table VII and those found in the Lesser Antilles are added for comparison.

TABLE VII.—American distribution of Antillean genera of spiders¹²

	Greater only	Greater and Lesser	Lesser only	Totals		
				Greater	Lesser	W. I.
Not on mainland...	7	2	9	9	11	18
S. A. only.....	5	5	19	10	24	29
C. A. only.....	2	1	1	3	2	4
U. S. only.....	4	2	1	6	3	7
S. A., C. A.....	6	10	6	16	16	22
C. A., U. S.....	6	2	1	8	3	9
S. A., U. S.....	4	2	3	6	5	9
S. A., C. A., U. S...	29	30	14	59	44	73
Total.....	63	54	54	117	108	171

¹² "C. A." includes Mexico, and "U. S." everything north of Mexico.

DISTRIBUTION OF SPECIES

Table VIII summarizes the data at hand. A few doubtful species have been omitted and several undescribed ones have been included.

TABLE VIII.—*American distribution of Antillean species of spiders*¹³

	Not on main- land	S. A. only	C. A. only	U. S. only	S. A. C. A.	C. A. U. S.	S. A. U. S.	S. A. C. A. U. S.	Total
Lesser only.....	88	18	2	2	4	2	1	4	121
P. R. only.....	6	2	2	1	1	..	12
Hisp. only.....	18	1	1	2	1	4	..	1	28
Cuba only.....	33	2	3	22	..	8	1	5	74
Jam. only.....	23	1	1	..	1	26
Less., P. R.....	9	..	1	..	1	11
Less., Hisp.....	1	1	2
Less., Cuba.....	3	2	..	1	2	8
P. R., Hisp.....	2	2	1	2	..	7
P. R., Cuba.....	2	..	2	1	..	2	..	2	9
Hisp., Cuba.....	5	2	..	3	10
Hisp., Jam.....	5	5
Cuba, Jam.....	1	1
Less., P. R., Hisp.	2	1	3
Less., P. R., Cuba	2	1	1	..	2	6
Less., Hisp., Jam.	1	1
P. R., Cuba, Jam.....	1	1
Hisp., Cuba, Jam.	1	1
Less., P. R., Hisp., Cuba.....	2	1	2	2	..	2	9
Less., P. R., Cuba, Jam.....	2	2
Less., Hisp., Cuba, Jam.....	1	1
P. R., Hisp., Cuba, Jam.....	..	1	2	..	2	5
All (?) Antilles.	1	3	4
Total.....	206	27	10	29	14	25	6	30	347

GENERAL DISCUSSION

IS THE FAUNA OF THE LESSER ANTILLES DISTINCT FROM THAT OF THE GREATER ANTILLES?

Comparing the two usual divisions of the Antilles—Greater and Lesser—we see that 50 per cent. of the Lesser Antillean genera of spiders, unfortunately meaning little more than the fauna of St. Vincent, have

¹³ Columns refer to the mainland and rows to the Antilles. "C. A." includes Mexico, and "U. S." everything north of Mexico.

not been found in the Greater Antilles and 53.8 per cent. of those known from the Greater Antilles have not been reported from the Lesser Antilles. In the Lesser Antilles 6.5 per cent. of the genera are peculiar and in the Greater, 5.1 per cent. In the Lesser Antilles 43.5 per cent. are strictly American and in the Greater, 42.7 per cent. The last two comparisons indicate considerable similarity in the general character of the two faunæ and raise doubt as to the significance of the fact that half of the fauna of each division is distinct from that of the other division. Do the two divisions have significantly distinct faunæ? Taking Hispaniola because it is in the midst of the Greater Antilles and bearing in mind that further study of the Hispaniolan spiders is more likely to bring out differences than similarities because we are now ignorant of the fauna of the interior, we note that 42.3 per cent. of its genera are not known from the Lesser Antilles, 44.3 per cent. are not known from Porto Rico, 30.8 per cent. are not known from Cuba and 65.4 per cent. are not known from Jamaica. The case of Jamaica is probably due, in large part, to ignorance and a further study of Cuba and Porto Rico without a further study of Hispaniola would doubtless reduce their figures, but it must also be kept in mind that data for the Lesser Antilles is largely drawn from an island well down the line, so that we must conclude that with respect to the genera of spiders the Lesser Antilles are no more different from the Greater Antilles than the different islands of the latter are from each other.

Of course, species show a much more limited geographic range than genera and the actual distance of St. Vincent from the Greater Antilles apart from purely faunistic factors becomes an important factor when considering species. There are 168 species known from the Lesser Antilles of which 72.0 per cent. are not reported from the Greater Antilles, and of the 226 species known from the Greater Antilles 79.2 per cent. are not known from the Lesser. In the Lesser Antilles 52.4 per cent. of the species are not known elsewhere and in the Greater Antilles, 42.5 per cent. It will thus be seen that the spider fauna of the rather isolated Lesser Antilles is not much, if any, more specialized than that of the Greater. Again taking Hispaniola for a basis of comparison we find that of its 76 species, 73.7 per cent. are not known from the Lesser Antilles, 68.4 per cent. are not known from the Porto Rican islands, 60.5 per cent. are not known from Cuba and 77.6 per cent. are not known from Jamaica. To say the least, the material at hand would not justify us in considering the Lesser Antilles any more distinct from the Greater than any of the islands of the Greater are from each other.

IS THE ANTILLEAN FAUNA DISTINCT FROM THAT OF THE MAINLAND?

The introductory paragraph to Scharff's Chapter on the origin of the West Indian fauna is as follows:

"North and South America are to be regarded, according to Professor Suess, as two essentially distinct land-masses, between which is interposed, as a third element, the area of Central America and the Antilles. This geological distinctness of Central America and the Antilles from the two neighboring continents is scarcely recognizable in the fauna of the great isthmus. But the West Indies are comparable to a wedge driven in between two faunistically, more or less, independent and distinct masses. Almost everyone who has dealt with the fauna or flora of the West Indian islands has expressed his surprise at this fact. In position, says Dr. Wallace, the Antilles form an unbroken chain uniting North and South America, in a line parallel to the great Central American isthmus. Yet instead of exhibiting an intermixture of the productions of Florida and Venezuela, they differ widely from both these countries, possessing in some groups a degree of speciality only to be found elsewhere in islands far removed from any continent."

Several years ago (1913) I published a brief note on the distribution of occidental spiders, getting the data entirely from Petrunkevitch's catalogue. As has been done here, I roughly divided the western hemisphere into four parts and found that 59.8 per cent. of the South American genera of spiders were not known elsewhere in America, 21.5 per cent. of those in Central America and Mexico were peculiar to that region and 37.5 per cent. of those from United States and Canada were not found farther south. Of the 133 Antillean genera then considered 13.6 per cent. were known only from the West Indies. The present paper includes 171 genera without adding any peculiar ones, so that the percentage is reduced to 10.5. This would also reduce the percentage for some of the other divisions but the figures as they stand are about as reliable as the data on which the revised ones would be based, genus being an indefinite sort of thing, so that we may conclude that the genera of spiders do not confirm the idea of the distinctness of the West Indian fauna. Instead of being very distinct from the mainland they are less so than any of the mainland divisions are from each other. Is this because spiders are more generally distributed than other animals or is the impression of distinctness an erroneous one based on a consideration of special cases?

The best way to settle the question of the distinctness of the Antillean fauna is to study carefully a number of groups which are fairly well represented in the Antilles and we are doing this in connection with the survey of Porto Rico which is being carried on under the auspices of the New York Academy of Sciences. Mammals were used by Wallace with

wonderful success but they do not seem to be good material for a West Indian discussion because there are so few of them. It is decidedly interesting that, except for bats, the Antillean mammals are rodents belonging to South American groups and *Solenodon*, a genus of Insectivora, whose nearest relatives are found only in Madagascar. These relationships will be referred to later but it may be noted in passing that such distributions are fairly common among spiders. The figures given by Wallace for birds show that about one-third of the Antillean genera are peculiar. This proportion is far greater than that for spiders and, when



FIG. 3.—Sandy plain south of Piñar del Río, Cuba

compared with the bird fauna of Central America, for example, shows a high degree of speciality, but Wallace's list gives only 95 genera of birds for the West Indies and there are more than 500 genera in Central America. The small number of vertebrates in the West Indies and the fact that a large proportion of those which are there are peculiar seem to be evidences of the unfitness of the Antillean environment for vertebrate life rather than of any special distinctness of the Antilles from the standpoint of geographic distribution.

It seems almost pedantic to point out the necessity of considering en-

vironment in a discussion of geographic distribution and yet it is almost never taken up in detail. There are several very practical reasons for this, two of which are well illustrated by this paper. First, there is already such a mass of detail that it can scarcely be handled and, second, the author is often, as in this case, ignorant of the ecological conditions under which the species occur throughout their ranges. The importance of ecological conditions may be illustrated in connection with what has just gone before as well as with what follows.



FIG. 4.—View near Baños San Vicente, Cuba

The level area is rich agricultural land, and even the cliffs support a rather luxuriant vegetation.

Mr. Leng and myself went to Piñar del Rio, Cuba, chiefly to study the ecological distribution of insects. We collected spiders in a number of environments, two of which are of interest here. South of the city is a sandy plain which we studied fairly intensively between the nine and thirteen kilometer posts on the road to Coloma. Leaving out of account the really important local differences caused by ground water level and the resulting differences in vegetation, figure 3 may be taken as fairly typical of the region. North of the city are the mountains and we col-

lected especially in the vicinity of Baños San Vincente. The difference in elevation between this place and the plains is not enough to cause a noticeable difference in temperature apart from that connected with soil conditions and moisture. Figure 4 gives an idea of the character of the region—moist atmosphere, lime-humus soil, rather “tropical” vegetation. Leaving out of account the Cohors *Araneus* and *Dendryphantes* for taxonomic reasons and not considering the minor ecological differences in each region, we found 10 genera on the plains which we did not find at Baños, 24 at Baños which we did not find on the plains and only 9 genera at both places. That is, 52.6 per cent. of the plains genera were not found in the hills and 72.7 per cent. of the hills genera were not found on the plains. In other words there is at least as much difference between these two nearby but ecologically different localities as there is between Cuba and the other islands or between the Antilles as a whole and the mainland.

Furthermore, this must give us a pause in considering the relationships of the various islands to each other and to the mainland, for 90 per cent. of the genera we took on the plains are found in United States and only 27.3 per cent. of those from the hills; 40 per cent. of the former are known elsewhere only in United States, as far as America is concerned, and only 4.5 per cent. of the latter. The general impression is that the West Indies are more closely related to Central and South America than to United States and, going still further, that the Lesser Antilles are especially related to South America and the Greater Antilles to Central America. If this be true, in how far is it due to land bridges, ocean currents or wind and in how far is it due merely to similarity, and hence congeniality, of environment? The first part of the question needs prior consideration, and the second part cannot be satisfactorily answered until we know more about animal ecology.

MAINLAND AFFINITIES OF THE ANTILLEAN FAUNA

As far as the data concerning the genera of spiders go, the Lesser Antilles (St. Vincent) seems to have a closer affinity with South America than does the other division of the Antilles, since 22.2 per cent. of the genera of the Lesser Antilles are known elsewhere in this hemisphere only in South America and the corresponding percentage for the Greater Antilles is only 8.6. However, if we include all the genera whose distribution we can study we note that only 82.4 per cent. of the genera known from the Lesser Antilles are known also in South America, while the corresponding percentage for the Greater Antilles is 84.3 per cent. The belief that work in the northern Lesser Antilles will still further

reduce the proportion of strictly South American genera in that division makes us somewhat dubious of there being any marked difference between the two divisions of the Antilles with respect to this relationship.

As far as the affinity between the Greater Antilles and Central America (including México) goes, we note that only 2.6 per cent. of the Greater Antillean genera are confined, in their American mainland distribution, to that region. Including all the genera, 13.5 per cent. of those known from the Greater Antilles are known also from Central America and Mexico, but the same percentage for the Lesser Antilles is 60.2, which is practically the same, in view of the fact that it is so largely based on the St. Vincent fauna.

As was pointed out several paragraphs before, Cuba has a number of genera known on the American mainland only from United States and Canada, but such genera represent only 5.1 per cent. of the genera known from the Greater Antilles (as a matter of fact, only 7.4 per cent. of the Cuban genera), while the same percentage for the Lesser Antilles is 2.8. Of the Greater Antillean genera 67.5 per cent. are known also in United States and Canada and 50.9 per cent. of those reported from the Lesser Antilles.

This, it seems to me, confirms the notion that, while individual genera differ, the general make-up of the spider fauna of the Lesser Antilles does not significantly differ from that of the Greater Antilles and that neither division has drawn from, or given to, any particular portion of the mainland much more than the other division.

A comparison of the Porto Rican spiders with those of the other islands brings out some interesting points. It has, as far as we know, no peculiar genera and only 9.8 per cent. of its genera are not known from the other Antilles. The data for the Lesser Antilles show 6.5 per cent. of peculiar genera and 50 per cent. which are not known from the other Antilles: for Hispaniola the figures are 3.8 per cent. and 17.3 per cent.; for Cuba, 1.2 per cent. and 29.3 per cent.; and for Jamaica, 6.6 per cent. and 20 per cent. The fauna of Porto Rico seems, then, to be of more recent origin than that of the other islands. This idea is strengthened by the fact that, while the differences are not great, only 30 per cent. of Porto Rican genera are strictly American as compared with 43.5 per cent. for the Lesser Antilles, 47.1 per cent. for Hispaniola, 38.3 per cent. for Cuba and 43.3 per cent. for Jamaica: also by the following, which is not strictly a restatement of the preceding, since a genus may be found in the Old World without being so widely distributed as to be classed as cosmopolitan. Cosmopolitan or cosmotropical genera make up 44.0 per cent. of the Porto Rican genera as compared with 20

per cent. for the Lesser Antilles, 41.2 per cent. for Hispaniola (practically, the port towns), 35.8 per cent. for Cuba and 33.3 per cent. for Jamaica.

Species also show the composite character of the Porto Rican spider fauna and are perhaps more convincing than genera. Only 8.7 per cent. of the Porto Rican species are peculiar as contrasted with 52.4 per cent. for the Lesser Antilles, 23.7 per cent. for Hispaniola, 25.2 per cent. for Cuba and 48.9 per cent. for Jamaica.

In view of this unusual character of Porto Rican spiders, it is worth while discussing their distributional affinities. Table VIII gives the data for the American distribution of species in a condensed form. Table IX shows the percentages of the total number of species in the several islands for various groupings.

TABLE IX ¹⁴

	L. A.	P. R.	Hisp.	Cuba.	Jam.
Peculiar.....	52.4	8.7	23.7	25.2	48.9
Not in other Antilles.....	72.0	17.4	37.0	56.5	55.3
In other Antilles but not on mainland.	13.1	29.0	27.6	13.7	21.3
On mainland but not in other Antilles.	19.6	8.7	13.2	31.3	6.4
On mainland (total).....	34.5	62.3	48.7	61.1	29.8

Porto Rico has as high a mainland affinity as Cuba and higher than the other islands, but it has a lower direct affinity (a lower percentage of species found on the mainland and not on the other Antilles) than any except Jamaica. That is, its fauna is largely mainland species which it has received by way of the other islands; Cuba's species are also largely mainland species, few of which have been passed on, while Jamaica has few mainland species and most of these have been received by way of the other islands or have been passed on to them. Of course, it would be possible for a species to originate in a West Indian island and then be transferred to the mainland and this may be true in Cuba. It would be impossible to determine from the data whether this has happened or not but it probably did not occur often enough to seriously complicate matters.

The rest of Table IX agrees with the idea just stated and repeats what was said before, as might be expected, since it is largely a complement of the two lines just considered. Porto Rico has the smallest percentage of endemic species of any of the islands or groups of islands; and, partly for this reason, but partly also because it has received a large proportion

¹⁴ For explanation, see text.

of its species from the mainland by way of the other islands, it has the smallest percentage of species which are not in the other Antilles. Porto Rico, Hispaniola and Jamaica contrast with the Lesser Antilles (St. Vincent) and Cuba in having a greater percentage of species which have originated in the Antilles and been passed to each other, but not to the mainland.

Table X gives the percentages of the species occurring in a given island and also on the mainland which are found in the several mainland divisions. It is an attempt to discover the way species have moved in relatively recent times. It probably concerns relatively recent movements only, for the species have not changed enough to lead taxonomists to give the mainland and insular lots different names. To be sure, we know that specific identity may be preserved for long geologic time and

TABLE X¹⁵

	Lesser	P. R.	Hisp.	Cuba	Jam.
S. A. only.....	31.0	11.6	10.8	3.8	14.3
C. A. only.....	5.2	7.0	2.7	6.3	7.1
U. S. only.....	6.9	7.0	10.8	30.0	0.0
S. A., C. A.....	17.2	14.0	8.1	6.3	7.1
C. A., U. S.....	8.6	20.9	29.7	21.3	14.3
S. A., U. S.....	3.4	7.0	5.4	2.5	0.0
S. A., C. A., U. S.....	27.6	32.6	32.4	30.0	57.2
Total S. A.....	79.3	65.1	56.8	42.5	78.6
Total C. A.....	58.6	74.4	72.9	63.8	85.7
Total U. S.....	46.5	67.4	78.3	83.8	71.4

experimental work has indicated that a species may arise not only suddenly but in several quite independent centers. However, most of the species considered here probably arose in relatively recent geologic time and each in a single center. Jamaica is troublesome because 33 (all but 14) of the species known from there do not occur on the mainland. Cuba has 51 such species; Hispaniola, 39; Porto Rico, 26, and the Lesser Antilles 110.

Except for the strictly South American species in St. Vincent and the strictly northern species in Cuba a large part of the species which are found in the various Antilles and also on the mainland are wide ranging on the mainland, being found in all three of its divisions. This may be due to the greater chance they have of getting to the Antilles (supposing they originated on the mainland) because their mainland distribution

¹⁵ For explanation, see text. Based upon 58 species in the Lesser Antilles, 43 in Porto Rico, 37 in Hispaniola, 80 in Cuba, and 14 in Jamaica.

puts them on three sides of the Antilles or, as is more probable, they are species which can live in a wide range of environments, as is indicated by their wide geographic range, and so have found it easy to establish themselves in the Antilles.

The Central American affinity is really slight. Although in the totals it seems to be important, an examination of the more detailed part of the table shows that this is caused by the groups in which it is joined with either the northern or the southern division or with both. For example, the 17.2 per cent. of the mainland species in the Lesser Antilles which are credited to South America and Central America should probably be credited to South America as is indicated by the fact that 31.0 per cent. are known on the mainland only from South America. The 5.2 per cent. which are known from the mainland only in Central America are three species which may have come directly from Central America but they more probably occur in South America or did recently occur there. Jamaica is the only island with a greater percentage of species which, as far as we know, are strictly Central American, than it has of species which seem to be confined to one of the other mainland divisions, but this percentage is misleading also as it represents but one species.

Presumably these species have reached their island homes from the mainland or have originated in the islands and spread to the mainland since the various islands have been separated, if, indeed, the islands were ever joined. The fauna of the islands at the ends of the Antillean chain have their strongest affinities with that part of the mainland which is nearest to them partly because of their geographical contiguity but partly also because of resemblance of habitat, witness the Floridian affinity of the fauna (and it is true also of the flora) of the sandy plains near Piñar del Rio, Cuba, as compared with the more tropical character of the mountains to the north of the city. If these species have spread themselves in this way without the aid of actual land connection, is such connection indicated in the older units, the genera?

It is doubtless clear that if we take all genera and treat them as we have just treated the species the result would be influenced by the inclusion of recently introduced species. Probably—but certainly not necessarily—those genera which have species peculiar to the Antilles have been on the Antilles longer than those whose only Antillean species occur also on the mainland. Table XI gives the percentages of such presumably old genera occurring in a given island and also on the mainland which are found in the several mainland divisions. It is an attempt to discover the way the fauna moved in relatively remote times.

TABLE XI ¹⁶

	Lesser	P. R.	Hisp.	Cuba	Jam.
S. A. only.....	21.1	6.9	9.4	10.2	5.9
C. A. only.....	2.8	3.4	6.3	4.1	11.8
U. S. only.....	4.2	3.4	0.0	6.1	0.0
S. A., C. A.....	21.1	17.2	21.9	18.4	11.8
C. A., U. S.....	4.2	3.4	3.1	4.1	17.7
S. A., U. S.....	7.0	3.4	6.3	6.1	0.0
S. A., C. A., U. S.....	39.4	62.1	53.1	51.0	53.0
Total S. A.....	88.8	89.7	90.6	85.7	70.6
Total C. A.....	67.6	86.2	84.4	77.6	94.1
Total U. S.....	54.9	72.4	62.5	67.3	70.6

As with species, a large part of the genera which are found on the various Antilles and also on the mainland are wide ranging on the mainland, being found in all three of its divisions. A part of this is, of course, due to those genera containing wide ranging species which also have species peculiar to the Antilles. We also note that, as with species, the strongest generic affinity of St. Vincent is with South America and probably most of the 15 genera (21.1 per cent.) found in both South and Central America got to or from Central America by way of South America.

It has already been pointed out that the Porto Rican spider fauna is largely recent. The data for genera as well as that for species indicates that its affinity is probably strongest with South America. It would not be profitable to discuss Hispaniola at length until we know more of the fauna in the interior, but it is interesting to note that no strictly United States genera have been found, and it is safe to predict that further study of Hispaniola will show it to be even more South American than is Porto Rico.

Cuba has a surprisingly small percentage of United States genera if we leave out of account the wide ranging ones. The facts that 30.0 per cent. of the species which are found on the mainland are not found on the mainland south of the United States as compared with 6.1 per cent. of presumably old genera, and that the figures for those not found north of South America are 3.8 per cent. and 10.2 per cent. respectively indicate that the older fauna has a stronger South American affinity than the more recent. The meaning of this will be discussed presently.

There are only 17 genera in Jamaica upon which to base the percentages given in Table XI. A strong affinity with Central America in ancient

¹⁶ For explanation, see text. Based upon 71 genera in the Lesser Antilles, 29 in Porto Rico, 32 in Hispaniola, 49 in Cuba, and 17 in Jamaica.

times is indicated, but as it is based on but 2 genera found on the mainland only in Central America and Mexico, 2 found in these regions and South America and 3 found in these regions and United States, it would not be safe to place much reliance on these data. Furthermore such affinity does not demand a land bridge; it may merely be a result of geographic contiguity and environmental similarity. If Jamaica has always been isolated as it is now, or at least if its last complete submergence was a long time ago and it has since been as isolated as it is now, we can understand the apparent poverty of its fauna, the peculiarity of it and its only slightly stronger affinity with Central America than with the other mainland divisions.

The impression all these things make on me is that the various Antilles may always have been as distinct as they are now; that they received their spider fauna by slow "accidental" means, and that Porto Rico has only recently been populated. How, then, are we to explain the ancient character of a large part of its fauna and the curious relationships with distant Old World localities? Also, why is the ancient portion of the Cuban fauna more South American than the recent?

ORIGIN OF THE ANTILLEAN FAUNA

Before considering further the origin of West Indian spiders it would be well to note their means of dispersal. Young spiders of nearly, if not quite, all families are more or less given to "ballooning." They will face against the wind, and, elevating their spinnerets, spin a quantity of fine silk usually in the form of a number of threads. These threads float in the breeze and finally they are numerous enough or long enough to carry their makers on an aerial journey. The length of such journeys would seem to depend very largely on the strength and character of the wind. McCook has attempted to show by its distribution that *Heteropoda venatoria* has circumnavigated the globe. It is true that the range of this species corresponds "with remarkable exactitude" to the belt over which the Trades blow, but we may accept his proof that the species has not been distributed by commerce without adopting his suggestion that its cosmotropical distribution is due to its ballooning habit. He cites Darwin's note about the "Beagle" being boarded by "flying" spiders when sixty miles from land and adds a report which is similar except that the latter ship was more than two hundred miles from land. It must be admitted that wind may be a very efficient factor in the distribution of many organisms, and it should be noted that when spiders go on such journeys they often go in swarms, so that it would not be unlikely that opposite sexes would land near enough each other to continue the species.

However, there is more to the distribution of spiders than wind. We need an explanation of the remarkable discontinuities which have been pointed out.

Ocean drift is frequently brought in to explain distribution and it has probably been the effective agent in many instances. The opponents of such an idea forget the long ages in which accidental drift has had a chance to work. However, the ease with which large numbers of spiders take to the air every year makes recourse to the small numbers that may make successful voyages on driftwood unnecessary.

Then there is man. Hardly a ship sails from port without araneid stowaways, and inland shipments of freight also carry their quota, but these are nearly always a certain few species of which only those that live about man's dwellings are likely to become established. None of the "tarantulas" which come in nearly every shipment of bananas have become a part of the New York fauna. Furthermore it is very unlikely that the distribution of most spiders has changed much since man began to sail the seas. The study of their movements must go far back of that.

One takes up the question of land bridges with something akin to a groan since opinion on the matter is so diverse and the evidence, whether pro or con, about a given bridge is often so slight. Paleontology offers little direct evidence as to the ancient movements of spiders since so few fossil spiders are known. Several have been described from the Carboniferous of both hemispheres and probably at least one genus (*Arthrolycosa*) was even then found in both Europe and North America. The only living genus of the type of spiders which was apparently common in Carboniferous is *Liphistius*. It is found now only in the islands of Pinang and Sumatra.

Spiders with unsegmented abdomens, that is all living spiders except *Liphistius*, may not have arisen until the Mesozoic, but, if so, evolution was fairly rapid, for most of the Oligocene and Miocene spiders belong to present-day families and even genera.

R. T. Pocock¹⁷ gives an interesting analysis of the ancient movements of spiders. A few of the present-day distributions given by him differ from those given by other authorities, but none of the differences which I have noticed would materially change his argument. In his section on the "Distribution of some of the Families of Arachnomorphæ that were represented in the Oligocene Period" he mentions seventeen genera found in amber which are still living. While it is perfectly true that "although since the Oligocene these Spiders have had the same time for dispersal, they nevertheless differ greatly in their distribution," the implication that

¹⁷Proc. Zool. Soc. London, 1903, I, pp. 340-368.

their present distribution is a measure of their success in extending their range does not necessarily follow. It is altogether probable that spiders fairly covered the earth in Oligocene times, and the few that were imprisoned in Baltic amber tell us nothing more than that they lived in that region, among others, at that time. It is pleasing to note that Pocock did not think it necessary to throw a bridge from continent to continent on the shortest line (according to Mercator's projection) between any two portions of a present-day discontinuous range. He naturally found considerable evidence of transfer in Arctic regions¹⁸ and he also used, rather freely, Antarctic connections between South America, Africa and Australia.

F. Dahl¹⁹ has considered the distribution of spiders and concluded that the Antarctic connection is improbable. Not all of his arguments seem to be well founded. For example, one can not consistently uphold the "relict" idea and then combat the Antarctic connection on the ground that so few relicts are found on the Antarctic islands. Most of the spiders, for the explanation of whose distribution an Antarctic connection might be desired, are tropical. It is therefore not surprising that relicts are not found on Antarctic islands.

It is no more than ordinary common sense to favor the simplest adequate explanation of a problem. It is unnecessary to review the voluminous literature concerning Antarctic connections between the three southern continents. It is admitted that many facts favor such connections, especially the one between South America and Australia, and that nothing has been, or is likely to be, brought out which will absolutely disprove it. However, if a simpler explanation than the general elevation of more than 3,000 meters required to connect South America and Australia, but which leaves Africa still to be accounted for, is adequate it would seem to be preferable. The final court of appeals is, of course, fossils, especially those in Antarctica, but even if numerous fossils are found in Antarctica and they are seen to be similar to those found in the southern portions of the other continents it will not prove actual connections. It will merely show that there has been an interchange of fauna—a thing not at all unknown between absolutely unconnected land areas and a thing for which there was a vastly longer time than we ordinarily have in mind since it requires a strong effort for us to bring ourselves to thinking in terms of millions of years.

¹⁸ The theory that practically all Tertiary migration was by way of the Arctic regions has been set forth most clearly by W. D. Matthew. It is amplified and convincingly discussed in his recent paper on "Climate and Evolution," *Annals N. Y. Acad. Sci.*, Vol. XXIV, pp. 171-318. 1915.

¹⁹ *Zool. Anzeiger*, vol. XXXVII, pp. 270-282. 1911.

In addition to, and partly because of, our relative ignorance of ancient spiders, we know but little of araneid phylogeny. We do know that spiders were already fairly well distributed, at least in the northern hemisphere, in the Carboniferous. Modern families and even genera were well differentiated in Oligocene. Therefore, as far as distribution problems are concerned, the present-day distribution of primitive genera in a given family or even primitive species in a given genus is of as much, or more, importance as the present-day distribution of primitive families. We unfortunately lack a sufficient knowledge of the compara-



FIG. 5.—Distribution of *Archæidæ*

A, Fossil (amber) *Archæa*; B, Living *Archæa*; C, *Mecysmauchenius*.

tive anatomy of spiders to enable us to use such data in the solution of the problems of distribution. In fact, widely discontinuous distribution is, at present, the best indication we have of relative antiquity and its use is rendered hazardous by reason of the possibility of polyphyletic origins—a possibility which has been rendered more probable by recent work in experimental evolution.

An analysis of the distribution of the world's spider fauna would be out of place in this paper and only a few points which seem to have a bearing on the West Indian problem will be taken up.

The family *Archæidæ* is an interesting one in this connection (see figure 5) since Baltic amber contains a genus (*Archæa*) of which the

only known living representatives are in Madagascar. Furthermore, the only other genus of the family is confined to Patagonia. Had it not been for the fortunate find in Baltic amber we would not know that the family ever occurred in the northern hemisphere and a land bridge from Patagonia to Madagascar in the most direct way compatible with sea-bottom contours would receive additional strong support. As it is, it seems more probable that this was once a fairly widespread family and it certainly occurred in northern Europe. We know that prior to the glaciers the climate of the North Polar regions was mild or even tropical

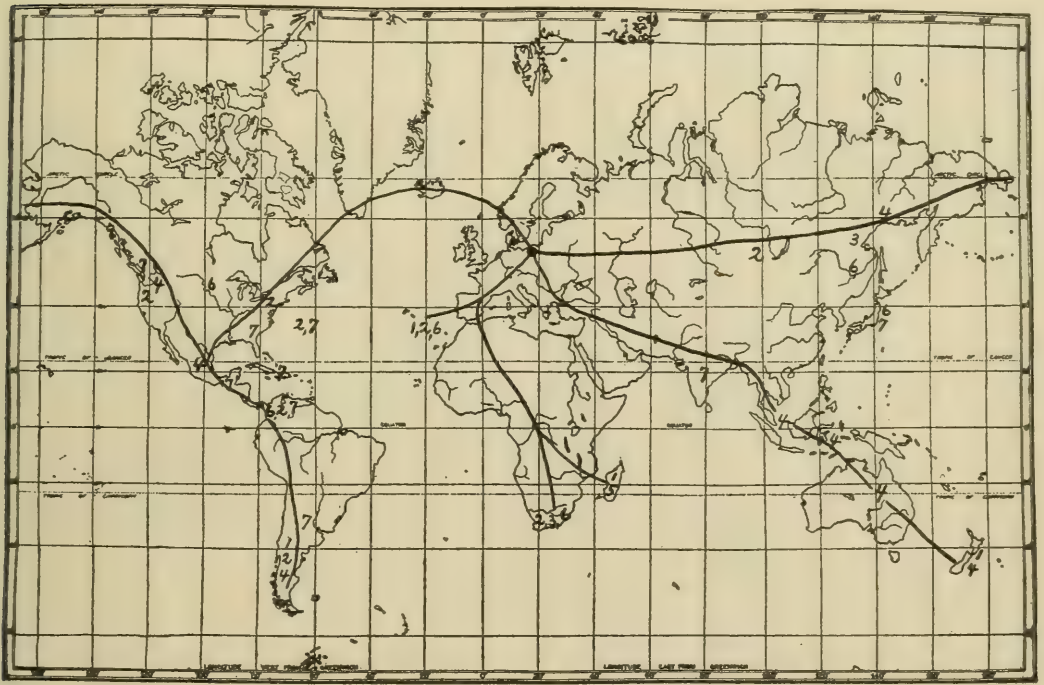


FIG. 6.—Distribution of certain genera known from Baltic amber

1, *Segestria*; 2, *Dysdera*; 3, *Eresus*; 4, *Amaurobius*; 5, *Archæa*; 6, *Agelena*; 7, *Anyphæna*. Only certain points in some of the ranges are indicated. The lines represent possible routes of dispersal.

and hundreds of circumpolar species point to the interchange of fauna between Eurasia and North America, where land bridges, if they ever existed, would not need to be long, so that it really seems quite probable that the genera of *Archæidæ* which are found in Madagascar and Patagonia respectively are merely remnants either of a formerly widespread family or of a northern family which was driven south by competition with new forms. Such a movement is supported by mammalian fossils and seems more likely than a South Polar connection.

Reference has been made to Pocock's list of seventeen recent genera found in Baltic amber. Of these we cannot consider here *Aranea* and

Zilla because their taxonomy is too unsatisfactory. *Drassus* has been split up by authors but even one of its parts is practically cosmopolitan. *Tetragnatha*, *Tegenaria* and *Philodromus* are cosmopolitan, even including frigid regions. *Clubiona* is found throughout most of the temperate and tropical regions; *Nephila* and *Sprassus* are cosmotropical; and *Thomisus* is found throughout most of the continental, at least, Old World. Certain points in the ranges of the other seven genera are shown in figure 6, only those most distant from the Baltic together with several intermediate stations being indicated. The supposition that all these seven



FIG. 7.—Distribution of *Segestriinae*
Lines refer to *Segestria* and dots to *Ariadna*.

genera originated in the Baltic region in, say, the Eocene would be absurd, but supposing that they did, would not the several million years since then, including as they do a long space of mild or tropical conditions in the Arctic, have been sufficient for the dispersal of these genera more or less along the lines indicated in the figure? I feel that even the rather well authenticated land connections in the North Polar region would not be necessary, for we must remember that the distances are much shorter in the polar regions than they appear to be on a Mercator's projection. Certainly, there seems to be no need for Antarctic connections. The distribution of *Archaea* has already been mentioned. The only other genus of special note is *Segestria*. The discontinuity of its

distribution is toned down by a consideration of *Ariadna*, a genus which with it forms the subfamily Segestriinae. Thus *Segestria* in New Zealand is linked with Asia by *Ariadna* in Australia, Sumatra and Ceylon. See figure 7.

By selecting certain genera or groups of genera of spiders it would be easy to make quite a list in favor of a land bridge from South America to Africa and elsewhere such as that shown in figure 8 which is after A. E. Ortmann's idea of certain of the connections in Upper Cretaceous times. For example the following genera might be cited: *Cyatholipus*

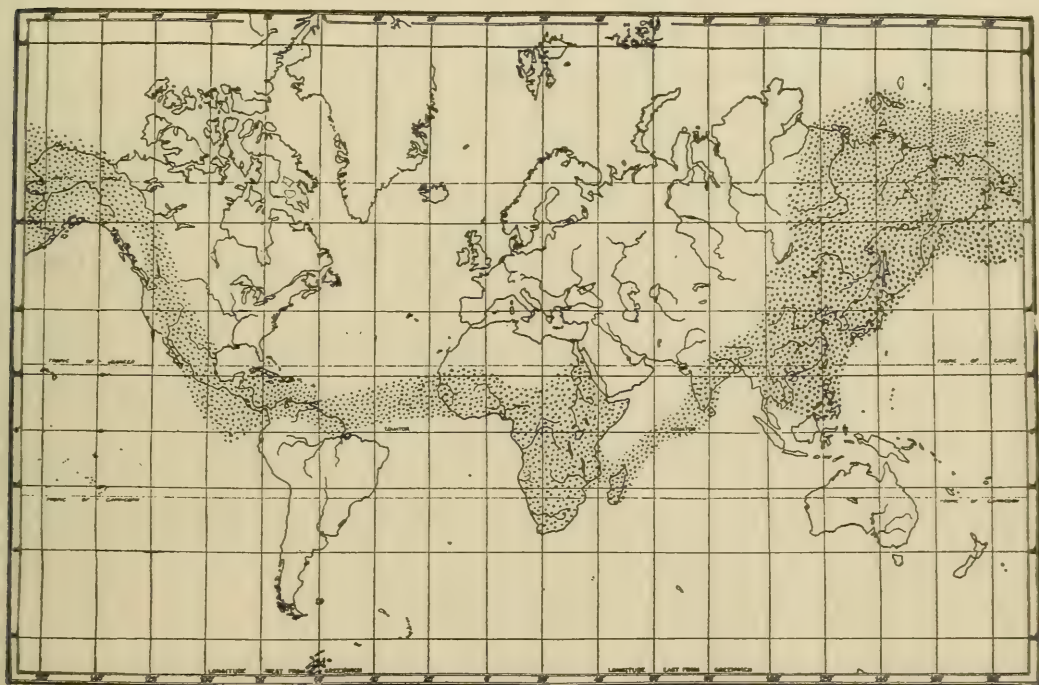


FIG. 8.—One of the hypothetical Upper Cretaceous land masses

and *Drymusa*, Antilles and South Africa; *Ischnothyreus*, Antilles, West Africa, Ceylon and Philippines; *Caloctenus*, Antilles, West Africa and Malasia; *Dyschiriognatha*, Antilles, Venezuela, Egypt, Ceylon, Borneo and Japan; *Opopaea*,²⁰ Antilles, Peru, Colombia, Venezuela, Africa, Arabia, Ceylon and Philippines; *Anapis*, Antilles, Venezuela, Brazil, northwest Africa and New Caledonia; *Ogulnius*, Antilles, Brazil and Ceylon; *Episinopsis*, Antilles, Peru and Malay Peninsula; *Theotima* and *Accola*, Antilles, Venezuela and Philippines; *Beata*, Antilles, Mexico to Brazil and Africa; *Syrisca*, Colorado, Utah, Texas, Brazil and Africa; *Oxyopeidon*, Arizona to Panama, Antilles, East Africa, India and Indo-

²⁰ Indeed the range of one species (*O. deserticola* Simon) is St. Vincent, Venezuela, Egypt, Arabia and Philippines.

China: *Ochyrocera*. Pacific coast states, Mexico. Antilles, Venezuela, Brazil, Ceylon and tropical Asia; and *Physocyclus*. California, Arizona, and New Mexico to Colombia, Guiana, Antilles, Africa and tropical Asia. All of these are on this particular hypothetical land mass and not elsewhere, as far as is known, except possibly several Peruvian or Brazilian localities. They were picked in a rather random fashion and only Antillean genera were included. Taking the world as a whole the list could be increased beyond the patience of the reader, but what would it prove? In general, it proves that it is possible to select a long list of genera and even some species which accord with a certain hypothetical land mass. In particular, the tropical parts of the area selected here includes some of the most important preserves of ancient types. We may leave polyphyletic origin of genera out of account not only because its occurrence is unproven but because it would not influence the case since a similar base from which to get the separate origins would be required and hence the problem would be merely restated, not changed. We have then to decide as to which is more reasonable: (a) forms migrated over this hypothetical land mass, which crosses the Indian Ocean and the Atlantic at the Equator, and then died out or have not been found except in certain favored spots on this mass; or (b) forms spread over land which now exists and, if you please, the shorter land connections but not the oceanic ones, and have died out or have not been found except in certain favored spots. A very readable and fair summary of the arguments in favor of the first alternative is given in Scharff's "Distribution and Origin of Life in America." He also favors a second Atlantic land mass running from the Antilles to the Mediterranean region with an offshoot to Bermuda and Nova Scotia. A list of spiders may be compiled from the taxonomic part of this or other papers which will accord with this bridge. The bridge was supposed to have existed in early Tertiary and to have also connected northeastern America by way of the Great Lake and Rocky Mountain regions with the southern tip of South America. Most of South America was under water; eastern Brazil and part of the present Atlantic bed formed a large island, while part of Ecuador and Peru formed the tip of a peninsula from the main land mass which lay in what is now the Pacific and included the Galapagos, a strip running across the middle of Central America to the Antilles, and in its northwestern sweep reached from California to Hawaii, but just before it got to western Canada it turned west, missed Alaska and connected up with Asia. The thing is rather complicated but certain spiders might have traveled the route. Note in this connection that several genera and groups of genera are known from northeastern North America and Pata-

gonia but are only poorly or not at all represented elsewhere. However, is it necessary? I think not. Even with ocean bottoms raised to form connections where connections are wanted and present continents sunk to explain the absence of forms where they are not found, one must further make all the assumptions required for the theory that distribution has been accomplished by present-day land masses. Forms either originated in America and passed to the Old World by way of the Arctic or the movement was in the reverse direction or, as is more probable, both are true. If geology demonstrates that there were land connections there, the passage will be seen to have been easy. However, there is no necessity for such connections since the distances are short and the time was long. The more recent American forms probably originated, for the most part, in America. The cutting off of the Arctic route by the lowering of the temperature has temporarily, at least, prevented natural interchange between the two hemispheres. Those recent forms which originated in the north are adapted to temperate conditions (which includes more than mere ability to withstand cool winters) and they have replaced in the north the old fauna which was adapted to more tropical conditions. In the south there are numerous remnants of this old fauna together with recent offshoots of it. The only assumptions necessary for this theory are really statements of fact, namely, that the climate of the Arctic was at least mild in the Tertiary and that many formerly wide ranging forms are now restricted in their distribution.

SUMMARY

To summarize what seems to be the facts concerning West Indian spiders: there has been considerable movement between the individual islands and also between the mainland and the islands, especially at the two ends of the island chain, even in recent times when the islands were separate from each other and from the mainland. It is therefore unnecessary to suppose that such connections ever existed. Ancient forms have had a longer time to reach the islands than the more recent ones, they were adapted to a tropical environment, and the insular character of the area has protected them, hence a large part of the fauna consists of relicts as is shown by the relationships with South Africa, Madagascar, Ceylon, Australia and the Philippines. Recent forms are now mingling with and replacing the older forms.

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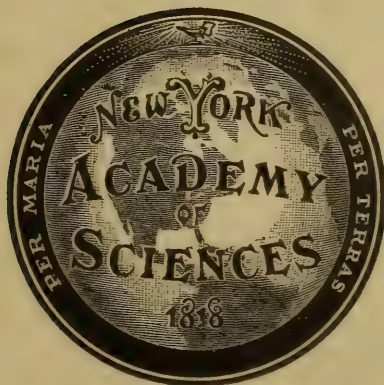
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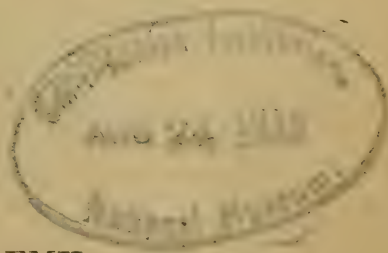
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VOLCANIC DUST VEILS AND CLIMATIC VARIATIONS¹

BY HENRYK ARCTOWSKI

(Presented in abstract before the Academy, 7 December, 1914)

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INTRODUCTION

The series of overlapping yearly means of temperature, expressed graphically, show most characteristic crests and depressions. In the case of tropical stations, in particular, the crests of the curves are very regular and occur at intervals of two to three years,² practically at the same time all around the world.

As a general result of a detailed study of the temperature data for the years 1900-1909, for Europe, Greenland and North America, I have found some striking correlations between these equatorial variations and the more complicated variations of temperate and arctic regions.³

In another study of all available temperature data for the years 1891-1900, I have shown that terrestrial atmosphere at the earth's surface was warmer in 1900 than in 1893 by at least 0.5 °C.⁴ On the maps representing the geographical distribution of the departures of annual means from the normals or from the quasi-normal values of ten-yearly means, the areas of positive departures have been called thermopleions

¹ Manuscript received by the Editor, 4 January, 1915.

² HENRYK ARCTOWSKI: "The Solar Constant and the Variations of Atmospheric Temperature at Arequipa and some other stations." Bull. Am. Geog. Soc., vol. 44, p. 598. 1912.

³ HENRYK ARCTOWSKI: "A Study of the Changes in the Distribution of Temperature in Europe and North America During the Years 1900 to 1909," Annals N. Y. Acad. Sci., vol. 24, p. 39. 1914.

⁴ HENRYK ARCTOWSKI: L'enchainement des variations climatiques. Bruxelles, 1909.

and the areas covered by negative departures antipleions. On the curves of overlapping means, the crests correspond to pleions and the depressions correspond to antipleions. I have presumed that the excess of pleions over antipleions, corresponding to pleionian crests of equatorial stations, may be due to an increase of the solar constant.⁵

Recently, many papers have been published about the influence of volcanic dust on meteorological phenomena, on atmospheric temperature in particular. I will simply cite the extensive researches of W. J. Humphreys,⁶ C. G. Abbot and F. E. Fowle⁷ and of H. H. Kimball.⁸ Humphreys, in particular, does not hesitate to admit "that volcanic dust must have been a factor, possibly a very important one, in the production of many past climatic changes."

The hypothesis ascribing the origin of climatic variations to the presence of volcanic dust veils in the higher atmospheric layers is a very plausible argument against my supposition that the changes in terrestrial temperature are due to cosmical causes. Before going any farther in my researches on the mode of formation and the dynamics of pleionian variations, it was therefore necessary to find out to what extent one may be justified in supposing that the antipleionian depressions of temperature are simply caused by the presence of volcanic dust veils.

In this paper I will show that though, in some cases, volcanic eruptions may have influenced atmospheric temperature very greatly, this cause of climatic variations is purely accidental and secondary, and that the pleionian phenomenon is independent, in its cause, of the occurrence of volcanic dust veils.

VOLCANIC ERUPTIONS OF THE YEARS 1883, 1902 AND 1912

Although we know, from geological records, that the volcanic activity of the earth's crust has undergone important changes, and although the historical data indicate that seismic and volcanic phenomena have varied in intensity and frequency, our knowledge of these fluctuations, of long as well as of short duration, is most unsatisfactory.

Papers on a possible relationship between sun-spots and volcanic phe-

⁵ HENRYK ARCTOWSKI: "About Climatic Variations," *Amer. Jour. Sci.*, vol. 37, p. 305. 1914.

⁶ W. J. HUMPHREYS: "Volcanic Dust and Other Factors in the Production of Climatic Changes and Their Possible Relation to Ice Ages," *Bull. Mount Weather Observatory*, vol. 6, p. 1. 1913.

⁷ C. G. ABBOT and F. E. FOWLE: "Volcanoes and Climate," *Smiths. Misc. Coll.*, vol. 60, No. 29. 1913.

⁸ HERBERT H. KIMBALL: "The Relation Between Solar Radiation Intensities and the Temperature of the Air in the Northern Hemisphere in 1912-13," *Bull. Mount Weather Observatory*, vol. 6, p. 205. 1914.

nomena have been published by E. Kluge,⁹ Joseph O'Reilly,¹⁰ Charles Zenger,¹¹ H. I. Jensen¹² and others. As will be seen later, a very suggestive conclusion may also be derived from the annual frequency list of volcanic eruptions compiled by Leo Kelley. If, therefore, some striking coincidences between changes of atmospheric temperature and the increase of frequency or violence of volcanic eruptions exist, the existence of these coincidences is a very inadequate argument in favor of the hypothesis that the variations of temperature are due to volcanic dust veils, since both phenomena, the volcanic paroxysms as well as the coincident temperature changes, may be the effect of some common extra-terrestrial factor.

In this study, however, only the volcanic eruptions of an explosive character have to be taken into special consideration. Moreover, it is only when volcanic dust has been projected in great quantity above the ordinary elevation of the cirrus clouds, that is to say to an altitude of 8,000 m. or higher up, that this dust could remain in suspension long enough to be spread out all around the globe by the winds of the lower stratosphere.

In the case of the famous Krakatoa eruption of 1883, the optical phenomena produced by the volcanic dust veil have been studied very extensively. For reference it will be sufficient to cite the reports of R. D. M. Verbeek¹³ and of the Royal Society.¹⁴

Krakatoa is a small island between Sumatra and Java and lies 6° S. lat. The explosion occurred on August 27, 1883. The main sky phenomenon produced by the dust went around the world in fifteen days from east to west along the equator, spread out north and south, was observed in the Gulf of Mexico by the end of September and all over the States in November. The extraordinary twilight phenomena have been well described by J. Kiessling.¹⁵ One of these phenomena, the Bishop's ring, has been the subject of many investigations.¹⁶ The actinometric

⁹ E. KLUGE: "Ueber einige neue Forschungen auf dem Gebiete des Vulkanismus," *Zeitsch. d. deut. geol. Ges.*, vol. 15, p. 377. 1863.

¹⁰ JOSEPH P. O'REILLY: "On the Dates of Volcanic Eruptions and Their Concordance with the Sun-spot Period," *Proc. Roy. Irish Acad.*, 3 ser., vol. 5, p. 392. 1899.

¹¹ CH. V. ZENGER: "La théorie électrodynamique du monde et les éruptions volcaniques et grands sismes," *Assoc. franç. p. l'avancement des sciences*, Sess. 33, p. 572. 1904.

¹² H. I. JENSEN: "Possible Relation Between Sunspots and Volcanic and Seismic Phenomena and Climate," *Jour. Roy. Soc. of New South Wales*, vol. 38, p. 40. 1904.

¹³ R. D. M. VERBEEK: *Krakatau*. Batavia, 1885.

¹⁴ G. J. SYMONS: *The Eruption of Krakatoa and Subsequent Phenomena*. London, 1888.

¹⁵ J. KIESSLING: *Untersuchungen über Dämmerungserscheinungen zur Erklärung der nach dem Krakatau-Ausbruch beobachteten atmosphärisch-optischen Störung*. Hamburg, 1888.

¹⁶ J. M. PERNTER: *Meteorologische Optik*, pp. 469, 769. Wien, 1902-10. See also —

SERENO BISHOP: "The Origin of the Red Glows," *Amer. Meteor. Jour.*, vol. 3, pp. 127, 193. 1886.

observations made by A. Crova,¹⁷ at Montpellier, have frequently been cited as a proof of the decrease of solar radiation due to a purely terrestrial cause. Curiously enough, the effect of the Krakatoa dust veil on atmospheric temperature seems to have attracted no special attention.

Besides the Krakatoa, other volcanoes were very active during the year 1883. Of these St. Augustin¹⁸ and Bogoslof¹⁹ of the Aleutian chain of islands, as well as the Ometepe,²⁰ may be mentioned.²¹ The violent eruption of St. Augustin, which occurred on October 6, is of particular interest. St. Augustin is an island south of the Alaskan peninsula (position— $153^{\circ} 25' W.$, $59^{\circ} 18' N.$). The explosion split the island in two, from peak to base, while the greater portion of the northern half of the volcano was blown away.

The study of the temperature data for the year 1902 is also of special interest, not only because during that year the world's volcanic activity was greatly intensified, but also because some of the explosive eruptions which occurred undoubtedly produced a dust veil in the higher layers of the atmosphere.

A decrease of solar radiation has been observed by Henri Dufour²² in Lausanne, by Harvey N. Davis²³ in Providence, by H. H. Kimball²⁴ in North Carolina, by S. P. Langley²⁵ in Washington, by L. Gorczyński²⁶ in Warsaw, and this decrease has generally been ascribed to the presence of volcanic haze.

In 1901 the outbursts of Mt. Colima, Mexico, were more frequent and more intense than during the preceding years. The same was true in

¹⁷ A. CROVA: "Sur les observations actinométriques faites à Montpellier," *Comptes Rendus*... vol. 106, p. 810. 1888.

¹⁸ GEORGE DAVIDSON: "Notes on the Volcanic Eruption of Mount St. Augustin," *Science*, vol. 3, p. 186. 1884.

¹⁹ C. HART MERRIAM: "Bogoslof, our Newest Volcano," *Harriman Alaska Expedition*, vol. 2, p. 291. 1901.

²⁰ G. MERCALLI: *Vulcani attivi della terra*, p. 356. Milano, 1907.

²¹ C. W. C. FUCHS: "Die vulkanischen Ereignisse des Jahres 1883," *Min. u. petrogr. Mitth.*, vol. 6 n. F., p. 185. 1885.

²² HENRI DUFOUR: "Sur la diminution du rayonnement solaire," *Comptes rendus*, vol. 36, p. 713. 1903.

²³ HARVEY N. DAVIS: "Observations of Solar Radiation with the Ångström Pyrheliometer," *Monthly Weather Rev.*, vol. 31, p. 275. 1903.

²⁴ H. H. KIMBALL: "Observations of Solar Radiation with the Ångström Pyrheliometer at Asheville and Black Mountain, N. C.," *Monthly Weather Rev.*, vol. 31, p. 320. 1903.

See also same author: "Solar Radiation, Atmospheric Absorption and Sky Polarization, at Washington, D. C.," *Bull. Mt. Weather Observatory*, vol. 3, p. 110. 1910.

²⁵ S. P. LANGLEY: "On a Possible Variation of the Solar Radiation and its Probable Effect on Terrestrial Temperatures," *Astroph. Jour.*, vol. 19, p. 305. 1904.

²⁶ LADISLAS GORCZYŃSKI: "Sur la diminution de l'intensité du rayonnement solaire en 1902 et 1903," *Compt. Rend.* ... vol. 138, p. 255. 1904.

Same author: "Quelques renseignements sur la dépression du rayonnement solaire à Varsovie en 1903," *Bull. Météor. du départ. de l'Hérault*. Montpellier, 1906.

1902 and even more so in 1903. The continuous observations of Mt. Colima made at the Zapatlan Observatory²⁷ from 1893 to 1905 give, for the years 1900 to 1904, the following frequencies of days during which eruptions designated "erupción grande" have been recorded: 15, 41, 37, 101, 2. According to C. G. Abbot,²⁸ a photograph taken on March 7, 1903, shows a column of ashes reaching an altitude of about 17 miles. This figure is a simple estimate and may be exaggerated.

On May 7, 1902, La Soufrière, St. Vincent, was in violent eruption. "The particular feature of this eruption was the enormous amount of dust which was thrown into the air and distributed over a vast, somewhat elliptical area. . . . The British steamship 'Coya' had an eighth of an inch of volcanic dust from this volcano fall on her deck when she was two hundred seventy-five miles east-southeast of St. Vincent."²⁹ On May 8, 1902, a sea of fire destroyed St. Pierre, Martinique. The following violent eruptions of Mt. Pelé occurred on May 20 and 26, June 6, July 9 and August 30.

The influence these eruptions may have had on the thermal transparency of the higher atmospheric layers is questionable. The excellent photographs taken by A. Lacroix³⁰ show indeed that the occasional blasts of incandescent gases and ashes did not exceed an altitude of 4,000 m. Only an extremely small portion of the projected pulverized ashes must have reached the average altitude of the cirrus clouds or even the stratosphere. This may not have been the case in the violent eruptions of the Santa Maria volcano, in Guatemala. The eruption began on October 24, 1902. An eye-witness writes: "During the first four days of the eruption no view could be had of the rising crater-cloud from the immediate vicinity of the volcano. Only at a distance of forty miles to the north and east could the erupted sand and smoke be seen against the sky. . . . Two days later I had another opportunity to view the eruption from a distant hill under a clear sky, and in the day. The appearance then was as follows: The peak of Santa Maria was sharply delineated against the sky. To the westward or oceanward of this pyramid rose every few minutes immense masses of globular clouds, like steam and smoke thrown out of a locomotive when it first starts. The clouds rose to a height of

²⁷ S. DÍAZ: *Efemerides del volcan Colima*. Mexico, 1906.

²⁸ C. G. ABBOT: "Do Volcanic Explosions Affect our Climate?" *Nat. Geog. Mag.*, vol. 24, p. 181. 1913.

JOSÉ MARIA ARREOLA: "Brief Notice of the Observations of Colima," *Jour. Geol.*, vol. 11, p. 751. 1903.

²⁹ EDMUND OTIS HOVEY: "Martinique and St. Vincent: a Preliminary Report upon the Eruptions of 1902," *Bull. Am. Mus. Nat. Hist.*, vol. 26, p. 333. 1902.

³⁰ A. LACROIX: *La montagne Pelée et ses éruptions*. Paris, 1904.

20,000 feet above the crater in three or four seconds." . . .³¹ The fall of ashes was observed principally in a northwestern and northern direction. In Chicharras, on the Mexican border, the thickness of ashes that fell on the ground was 420 mm., whereas in Oaxaca and San Juan Bautista only 5 mm. were observed.³²

The eruption of the Mua, on Sawaii of the Samoa Islands, which occurred October 30, 1902, was not violent enough to be taken into consideration.³³ The same may be said about the Isalco eruption, in Salvador.³⁴ On the contrary, the Tori-shima eruption of August 7 and 9, 1902, seems to have been very violent. Reports of this eruption have been published by F. Omori and others of the Imperial Earthquake Investigation Committee, but these publications were not accessible to the writer.

There can be no doubt that during the year 1902 a considerable quantity of pulverized lava must have been projected into the higher layers of the atmosphere, above the clouds. Bishop's ring was observed anew,³⁵ as well as extraordinary twilight phenomena;³⁶ but a comparison is hardly possible with those which were due to the Krakatoa eruption. One single volcanic explosion, if sufficiently violent, may therefore obscure the stratosphere very much more than a score of violent eruptions of a less explosive character.

This seems to have been the case of the Katmai eruption. "Katmai volcano is in the Aleutian Range, Alaska, latitude 58° N., longitude 155° W. approximately. On the afternoon of June 6, 1912, it suddenly became explosively eruptive, continued in a state of great activity for about three days, and was reported to be still somewhat active at the end of October, 1912."³⁷ For particulars I will refer to an account published

³¹ GUSTAV EISEN: "The Earthquake and Volcanic Eruption in Guatemala in 1902," *Bull. Am. Geog. Soc.*, vol. 35, p. 391. 1903.

³² KARL SAPPER: "Die vulcanischen Ereignisse in Mittelamerika im Jahre 1902," *N. Jahrb. f. Miner., Jahrg.*, 1904, vol. 1, p. 39. See also ALFRED BERGHEAT: "Die Produkte der letzten Eruption am Vulkan S. Maria in Guatemala," *Centr. f. Mineral., Jahrg.* 1903, p. 112.

³³ GEORG WEGENER: "Die vulkanischen Ausbrüche auf Sawaii," *Zeit. Gesell. f. Erdkunde zu Berlin*, p. 208. 1903.

³⁴ KARL SAPPER: "Die jüngsten Ereignisse am Vulkan Izalco," *Centr. f. Mineral., Jahrg.* 1903, p. 103. 1903.

³⁵ F. A. FOREL: "Le cercle de Bishop de la Montagne Pelée 1902-1904," *Arch. Sc. Phys. et Nat.*, Ser. 4, vol. 19, p. 229. 1905.

³⁶ P. GRUNER: "Ueber die neuen Dämmerungserscheinungen," *Mitt. naturf. Gesell. Bern.* a. d. J. 1903, p. 1. 1904.

E. MARCHAND: "Les lueurs crépusculaires et phénomènes connexes," *Annuaire Soc. Météor. France*, vol. 53, p. 40. 1905.

³⁷ HERBERT H. KIMBALL: "The Effect upon Atmospheric Transparency of the Eruption of Katmai Volcano," *Month. Weather Rev.*, vol. 41, p. 153. 1913.

in the *National Geographic Magazine*.³⁸ A summary of the effects of the Katmai eruption on atmospheric optical phenomena has been given by J. Maurer and C. Dorno.³⁹

The fact that the Katmai eruption occurred in a far northern latitude, and has not been followed by similar volcanic outbreaks in other parts of the world, is most valuable. Since the general atmospheric circulation of the southern hemisphere is independent of that of the northern hemisphere, it is difficult to imagine how the haze produced by the Katmai eruption could have been carried south of the equator. If therefore we observe, on the temperature curves of stations belonging to the southern hemisphere, great similarities in the details of the curves of stations belonging to the northern hemisphere, attributed to the presence of volcanic haze, it is evident that, however incomplete our knowledge of the general atmospheric circulation may be considered, the supposed volcanic dust influence must be discarded.

Some argumentation, however, leaves the question open for discussion. The correlations between the seasonal variations of far distant stations, first noticed by H. W. Dove⁴⁰, then later more extensively studied by H. F. Blanford,⁴¹ H. H. Hildebrandsson,⁴² J. Hann,⁴³ H. G. Lyons,⁴⁴ Felix M. Exner,⁴⁵ R. C. Mossman⁴⁶ and others, show that one may presume that an anomaly at one "center of action" of atmospheric circulation of one hemisphere will produce a similar anomaly at a corresponding station belonging to a correlated "center of action" of the other hemisphere. I suppose that the number of stations for which temperature records have been compared is sufficient to eliminate the possibility of such an argument.

³⁸ GEORGE C. MARTIN: "The Recent Eruption of Katmai Volcano in Alaska," *Nat. Geog. Mag.*, vol. 24, p. 131. 1913.

³⁹ J. MAURER and C. DORNO: "Ueber den Verlauf und die geographische Verbreitung der atmosphärisch-optischen Störung 1912-1913," *Meteor. Zeit.*, vol. 31, p. 49. 1914.

⁴⁰ H. W. DOVE: *Nicht periodische Veränderungen der Verbreitung der Wärme auf der Erdoberfläche*. Berlin, 1869.

⁴¹ H. F. BLANFORD: "On the Barometric See-saw between Russia and India in the Sun-spot Cycle," *Nature*, vol. 21, p. 477. 1880.

⁴² H. H. HILDEBRANDSSON: "Quelques recherches sur les centres d'action de l'atmosphère," *K. Svenska Vetensk. Akad. Handlingar*, vol. 29, no. 3, vol. 32, no. 4, vol. 45, no. 2, vol. 45, no. 11. 1897, 1899, 1909, 1910.

⁴³ J. HANN: "Die Anomalien der Witterung auf Island in dem Zeitraume 1851-1900 und deren Beziehungen zu den gleichzeitigen Witterungsanomalien in Nordwesteuropa," *Sitz. Math. nat. Kl. K. Akad. d. Wiss.*, vol. 113, II a, p. 183. Wien, 1904.

⁴⁴ H. G. LYONS: *The Physiography of the River Nile and its Basin*. Cairo, 1906.

⁴⁵ FELIX M. EXNER: "Ueber monatliche Witterungsanomalien auf der nördlichen Erdhälfte im Winter," *Sitz. K. Akad. Wiss. Math.-Naturw. Klasse*, vol. 122, II a, p. 1165. Wien, 1913.

⁴⁶ R. C. MOSSMAN: "Southern Hemisphere Seasonal Correlations," *Symons's Met. Mag.*, vol. 48. London, 1913.

PIKE'S PEAK TEMPERATURE RECORDS

The meteorological observations made on the summit of Pike's Peak extend through the years 1874-1887. It seems to me that the records of this station—situated near the center of the North American continent, at an altitude of 14,111 feet—may be considered as being most reliable material for the study of the influence of the dust veil of the years 1883 and 1884, upon temperature conditions in the United States.

Table I gives the recorded mean monthly temperatures (5 A. M., 1, 9 P. M.) expressed in departures from the corresponding monthly means of the entire series of observations.⁴⁷ In Figure 1 the consecutive twelve monthly means are represented graphically. On this diagram, one notices



FIG. 1.—Curve of the consecutive means of temperature observed on the summit of Pike's Peak

immediately that the curve is abnormal between the crests *C* and *E*, that in order to have a more regular variation, we ought to have a crest (*D*) in place of the depression *K*. Admitting the existence of such a crest, we have intervals of 33, 27, about 31 and about 35 months between the crests and 30, 33, 25 and 31 months between the depressions. These figures are similar to those obtained from the records of many other stations. But, as on the curves expressing the succession of consecutive means for longer series of observations—for example those of Batavia, New York, Rome, Warsaw and Stockholm, which are at present at my disposal—the pleionian crests do not always reoccur at approximately regular intervals and seem to be missing sometimes, just like the presumed crest (*D*), the fact that the Pike's Peak curve shows a long in-

⁴⁷ *Annals Astron. Obs. Harvard College*, vol. 22, p. 457. 1889.

TABLE I.—*Monthly means (°F.) observed on Pike's Peak and departures from these means for the years 1874-1887*

	Jan.	Feb.	March	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
	2°.3	3°.6	7°.8	12°.1	22°.5	32°.7	40°.0	38°.5	31°.4	21°.5	10°.8	6°.2
1874.....	+3.5	-3.9	-3.0	-4.5	+0.6	+1.2	+0.7	-0.4	-2.9	-0.9	-0.1	-0.2
75.....	-2.5	-3.9	-9.1	-1.7	-0.2	+1.0	-4.9	-2.8	+0.7	+3.8	0.	+3.6
76.....	+0.1	+1.2	-3.2	+2.8	-1.0	-1.9	+1.7	+0.1	+0.5	+0.1	+0.4	-1.2
77.....	+3.0	+4.3	+4.3	-2.5	-4.1	-4.6	-0.9	+0.9	-0.2	-4.5	-4.9	+0.4
78.....	-1.0	-1.1	+2.0	+0.3	-2.7	-2.6	+1.2	+3.8	-2.1	-1.0	+2.4	-6.7
79.....	+2.5	+3.3	+8.3	+4.7	+3.2	+0.6	+2.7	+0.4	+4.7	+4.7	+1.5	-2.0
1880.....	+4.2	-4.1	-2.8	+0.6	+1.3	+3.6	-1.8	-1.5	-1.0	-3.2	-10.7	+0.7
81.....	-2.7	+1.2	-3.1	-3.9	+2.8	+7.2	+3.3	+2.4	+0.2	+1.9	-3.6	+2.8
82.....	0.	+2.2	+0.4	+1.4	-2.6	-2.4	-1.7	-0.5	-2.0	-1.8	+2.5	+0.5
83.....	-4.2	+0.8	+5.2	0.	-2.9	-1.4	-0.9	+0.2	-1.2	-5.1	+3.0	+1.9
84.....	+0.1	-1.0	-2.9	-3.6	-2.1	-2.3	-0.2	-2.9	+0.6	+2.9	+2.5	-0.8
85.....	-0.9	-1.7	+1.6	+3.8	-1.4	-2.9	-0.7	-1.4	-0.4	-0.3	+3.0	+2.5
86.....	-0.3	+2.6	-3.8	0.	+4.6	+0.3	+2.5	+2.0	+1.2	+0.6	-3.7	+2.4
1887.....	-1.9	+0.4	+6.8	+2.6	+4.0	+3.6	-0.9	-0.5	+2.0	+2.4	+7.5	-4.0

terval between the crests *C* and *E*, of nearly six years or the double of the interval generally observed, cannot be considered as an argument in favor of a correlation between the temperature depression *K* and the eruptions of Krakatoa and St. Augustin. But the drop of temperature for the mean of November, 1882,-October, 1883, coincides with the appearance of the Krakatoa veil in the States and also with a possible influence of the St. Augustin eruption, so that a simple chance circumstance can hardly be admitted. Then the curve starts up, just as it went up before the consecutive mean ending with October, 1883, and this tendency is maintained for a few months. The small crest *d* in the depression *K* seems to be another detail showing clearly that this depression is abnormal, that it is not a true antipleionian depression.

Besides, on the table of monthly departures, we notice the exceptional figure—5.1 °F. for October, 1883, and the succession of negative departures for the year 1884.

In order to show that the depression *K* was really abnormal and that under normal conditions we ought to have had a pleionian crest (*D*) in place of this depression, I will consider now the consecutive temperature curve of Port Darwin, a station of North Australia, 12° 28' lat. S.

TEMPERATURES AT PORT DARWIN AND SOME OTHER STATIONS

In Table II the monthly temperatures for the years 1880-89 are given in departures from the means figuring on top of the table.⁴³ The diagram (Fig. 2) represents the succession of consecutive annual means.

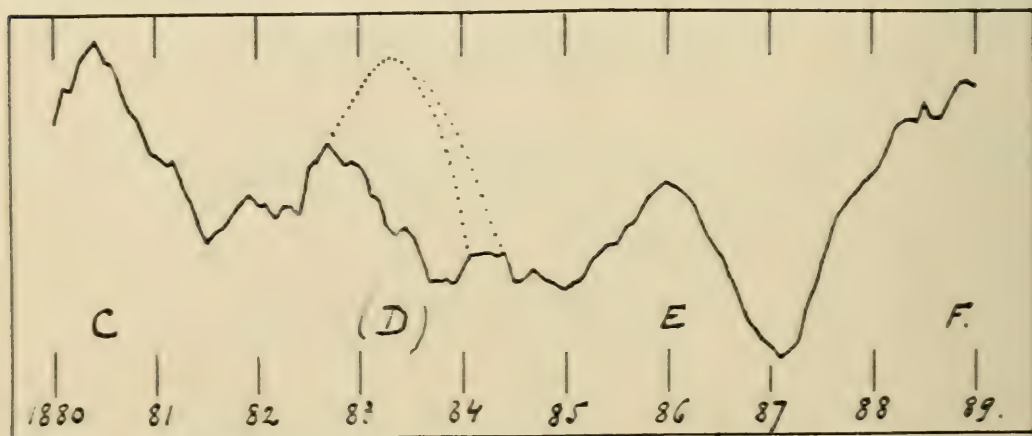


FIG. 2.—*Thermopleionian variation of Port Darwin*

A comparison of Figures 1 and 2 shows striking similarities between the two curves. I marked, therefore, the crests of the Port Darwin curve

⁴³ Meteor. Observat. made at the Adelaide Observatory...during the year 1880...1889.

TABLE II.—*Monthly means (°F.) of the daily maxima and minima observed at Port Darwin during the years 1880–1889 and departures from these means*

	Jan.	Feb.	March	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
1880.....	84°.5	83°.7	85°.3	85°.2	82°.3	79°.0	76°.9	79°.9	83°.2	85°.9	86°.4	85°.4
81.....	−2.2	+0.8	−0.3	+0.8	+1.3	+1.3	−0.4	+2.4	+1.4	+0.6	+2.4	+1.0
82.....	+2.3	+0.5	+2.7	+2.6	+2.5	−1.2	−0.9	−1.1	−0.9	−0.4	−1.0	(+0.4)
83.....	+1.5	+0.7	−0.3	+0.9	−0.6	−3.2	+0.3	−0.5	+1.2	+0.6	−0.1	−0.7
84.....	+1.5	−0.8	+1.1	+0.5	−1.5	+2.2	+1.7	+1.4	−0.5	−0.4	+0.1	−1.0
85.....	−1.9	−1.3	−2.1	−0.7	−0.9	+1.6	−1.0	−1.3	−0.4	−0.3	−0.4	+0.6
86.....	−0.2	−0.9	−2.1	−1.3	−0.6	−1.6	−0.9	−0.1	−0.8	−0.7	−1.2	−0.2
87.....	+0.7	−0.2	−0.1	−0.2	−0.1	−1.2	+1.1	+0.5	+0.9	+0.5	+0.1	+0.2
88.....	−0.2	−0.9	−0.7	−3.6	−1.7	−2.6	−1.4	−1.9	−1.8	−0.9	−1.2	−0.3
89.....	−1.7	−0.3	0.	+0.2	+1.1	+1.4	+1.3	+0.5	−0.2	−0.3	+0.4	+0.1
89.....	+0.1	+2.3	+1.9	+0.9	+0.8	+3.8	−0.2	+0.3	+1.6	+1.5	+0.8	−0.4

with the letters *C*, (*D*), *E* and *F*, expressing that way my view that the variations are identical.

However, a very important difference must be noted at once; it is the difference in time of the occurrence of the same pleionian crests and antipleionian depressions. The Pike's Peak maxima occur ten or eleven months later than those of the Port Darwin curve. Now, the distance between the crests *C* and *E* is in both cases 67 months. Some of the details of the crest *C* of Pike's Peak, as well as of the depression that followed, may be easily observed on the corresponding crest and depression of the Port Darwin curve. If, therefore, the missing pleion of the Pike's Peak curve appears very plainly on the Port Darwin curve, as it does, we are justified in presuming that the interval of more than 5 years separating the crests *C* and *E* on the Pike's Peak was indeed abnormal, as well as the depression *K*, and that this anomaly must be ascribed to the Krakatoa dust veil.

The crest (*D*) of Port Darwin is not developed to its normal value. On the diagram the dotted line indicates the portion which must be considered as having been cut away. The anomaly begins with the consecutive mean of October, 1882, to September, 1883, that is to say, just one month sooner than on Pike's Peak. This anomaly is not ten or eleven months in advance on the corresponding detail of the Pike's Peak curve, but just one month and occurs one month later than the Krakatoa eruption—when the dust veil reached Port Darwin, after having traveled twice around the world along the equator. The duration of the anomaly extends from the mean of October, 1882,-September, 1883, till the mean of February, 1884,-January, 1885, or 17 months. The same figure may be adopted in the case of the Pike's Peak curve.

An important question arises now. Is it possible to estimate the lowering of temperature due to the presence of the Krakatoa dust veil? According to the dotted lines of the diagrams the lowering of the temperature for the consecutive mean of September, 1883,-August, 1884, may have been 1.9 °F. in the case of Port Darwin and 3.4 °F. in the case of the Pike's Peak observations. But this is an estimate of no scientific value. The departures of Tables I and II are of no help. It would be necessary to know what these departures ought to have been. I imagine it would be possible to attempt the calculations by tracing maps and by comparison of the temperature conditions of the dust-affected regions with those over which the dust veil was not spread out. But even in that case comparisons would be most difficult, because we do not know how the dust veil affected the general atmospheric circulation or how the abnormal conditions of one region affected the temperatures of other regions mechanically.

The curve of the consecutive means of the temperatures observed at the Batavia observatory confirms the results obtained so far. So do the curves of Singapore, Port Blair, Colombo, Bombay and Aden,⁴⁹ which are reproduced in Figure 3.

The curves of Bombay and Port Blair show distinctly the antipleionian depressions preceding and following the abraded pleionian crest. At

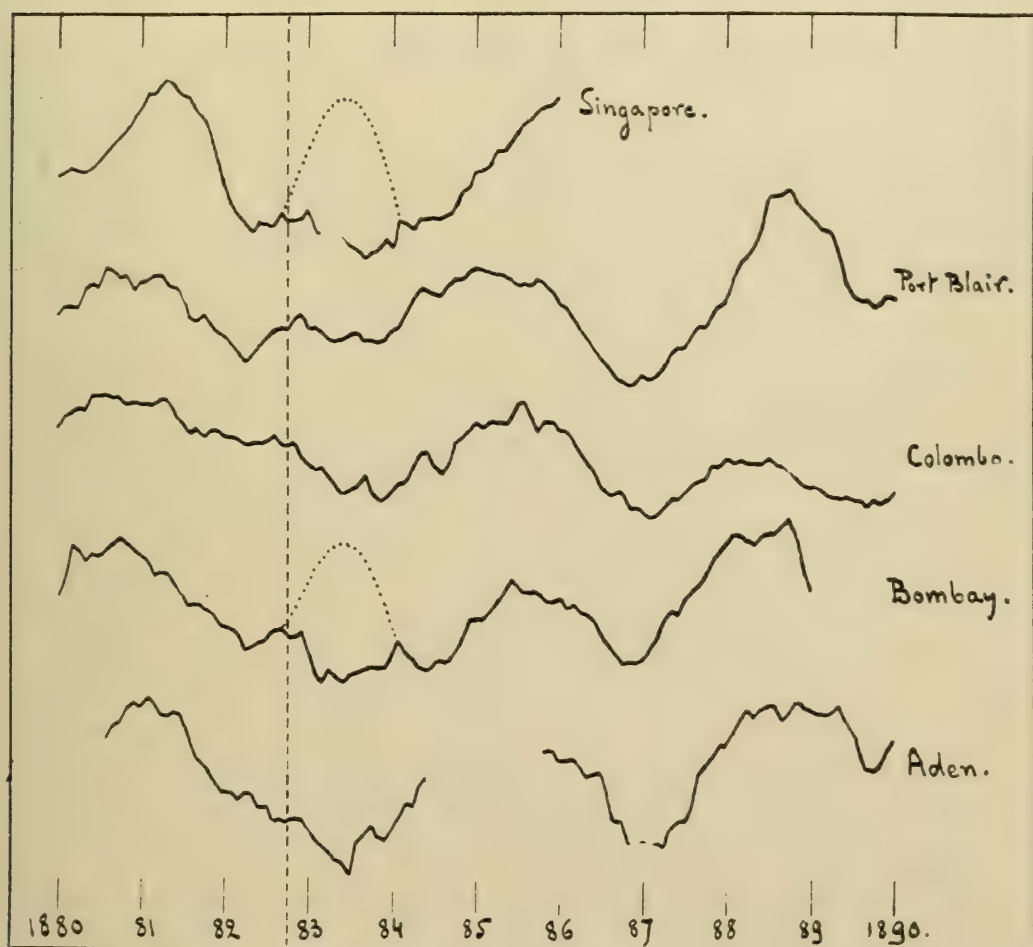


FIG. 3.—Temperatures recorded at some Asiatic stations

Port Blair the pleion is less depressed; at Aden the most. If the lowest mean of the two years following the Krakatoa eruption expresses the maximum effect of the dust veil, we must say that this maximum effect was not simultaneous at the different stations taken into consideration. The following tabulation gives the periods, as well as the lowering of the mean below the value of the last unaffected consecutive mean.

⁴⁹ Singapore from: "Met. obs. at the foreign and colonial stations of the Royal Engineers...1852-1886." London, 1890.

The other stations from: "Report on the meteorology of India in 1880...1890."

Pike's Peak.	Sept. 1883-Aug. 1884:	1 0 °F	below the mean of Sept. 1882-Aug. 1883				
Port Blair...	Dec. 1883-Nov. 1884:	1.4	" " " " " "	"	"	"	"
Bombay	June 1883-May 1884:	0 6	" " " " " "	"	"	"	"
Singapore...	Sept. 1883-Aug. 1884:	0 6	" " " " " "	"	"	"	"
Aden.....	July 1883-June 1884:	0.7	" " " " " "	"	"	"	"
Colombo....	Nov. 1883-Oct. 1884:	0.7	" " " " " "	"	"	"	"
Port Blair...	Nov. 1883-Oct. 1884:	0 2	" " " " " "	"	"	"	"

TEMPERATURES AT FORT-DE-FRANCE, MARTINIQUE

During the terrific eruptions of Mt. Pelé, on May 8 and 20, 1902, the usual meteorological observations were made at Fort-de-France. In Table III the monthly mean temperatures are given in form of departures from the corresponding means of the years 1900-1909 and in Figure 4 the curve *A* represents these departures graphically. Curve *B* shows the

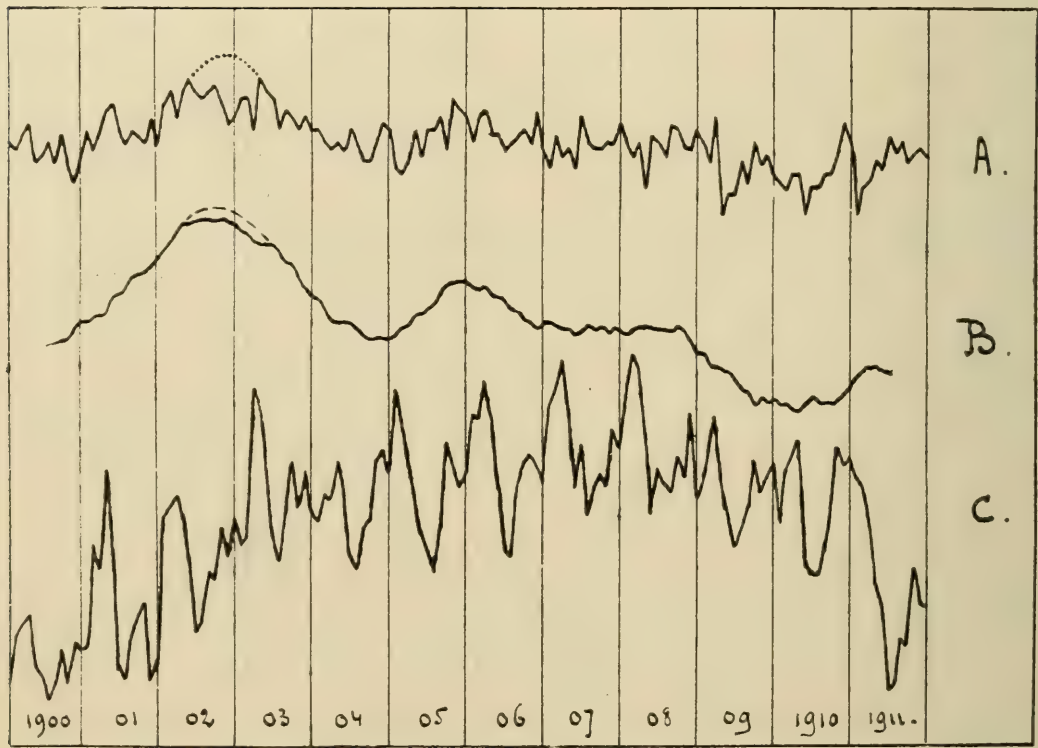


FIG. 4.—Temperature records at Fort-de-France

succession of consecutive yearly means and *C* gives the values of the differences between the monthly mean maxima and minima. This last curve indicates the changes of the range of the diurnal variation of temperature. On the average, the lowest value is observed in July and the highest in March. The respective mean values for the different months are: 8°.32, 8°.72, 8°.95, 8°.72, 7°.78, 7°.18, 6°.99, 7°.53, 7°.97,

TABLE III.—*Monthly means (°C.) of the maxima and minima temperatures observed daily at Fort-de-France during the years 1900–1909 and departures from these means*

	Jan.	Feb.	March	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
	24°.8	24°.8	25°.2	26°.2	26°.8	26°.8	26°.8	27°.1	27°.1	26°.9	26°.3	25°.4
1900.....	−0.1	−0.2	0.	+0.2	−0.4	−0.3	−0.1	−0.4	0.	−0.5	−0.7	−0.3
01.....	+0.1	−0.2	+0.1	+0.4	+0.5	+0.1	−0.1	+0.1	0.	−0.1	+0.3	−0.1
02.....	+0.5	+0.7	+0.3	+0.7	+0.9	+0.7	+0.6	+0.7	+0.8	+0.5	+0.2	+0.3
03.....	+0.6	+0.6	+0.1	+0.9	+0.7	+0.6	+0.1	+0.4	+0.3	+0.1	+0.3	+0.1
04.....	+0.1	−0.1	−0.2	−0.1	−0.2	+0.1	−0.1	−0.4	−0.4	−0.1	+0.2	+0.1
05.....	−0.5	−0.6	−0.4	+0.1	−0.3	+0.1	+0.1	+0.3	−0.2	+0.6	+0.4	+0.3
06.....	−0.1	+0.3	+0.4	0.	0.	−0.2	−0.1	0.	+0.1	−0.1	+0.4	−0.2
07.....	−0.5	0.	−0.3	−0.2	−0.5	+0.3	−0.1	−0.2	−0.2	−0.1	−0.1	+0.2
08.....	−0.1	−0.3	−0.1	−0.8	0.	−0.1	−0.3	+0.2	+0.1	−0.2	−0.2	+0.1
09.....	−0.1	−0.4	+0.3	−1.2	−0.9	−0.9	−0.4	−0.7	−0.1	−0.4	−0.3	−0.6

$8^{\circ}.14$, $8^{\circ}.17$ and $8^{\circ}.02$ C. Curve *C* indicates a long range variation completely independent of the temperature variation, which has a maximum in 1902 and a minimum in 1910, as can be seen on curves *A* and *B*. The data which I collected some years ago from the observations of Russian stations⁵⁰ give the result that these long-range variations of the values of the mean diurnal oscillations of temperature differ from one region to another and that these variations correspond to changes of cloudiness. An increase of cloudiness diminishes the average daily range of temperature. Considering now the trend of the curve we notice a more or less progressive increase of the values from 1901 to 1904. This is just the contrary of what would be expected. At Fort-de-France the daily range of temperature has therefore not been greatly affected by the dust veils produced by the eruptions of Mt. Pelé, Sta. Maria and Mt. Colima.

The mean temperatures have also been affected but very slightly. The pleionian crest of 1902-1903, as indicated on the curve of consecutive means, has been depressed a little, but certainly not more than 0.15° C. or 0.2° F. It is difficult to judge how much the mean temperatures of the individual months have been affected. Curve *A* shows a decrease of the departures for the months of June, July and August, 1902, following the great Mt. Pelé eruption; also a more pronounced decrease for November and December, possibly due to the Sta. Maria eruption, and finally the low April departure may have been caused by the Colima eruptions. However the departures of the months of May, 1902, to the end of 1903 are all above the average and if the slight deflections observed during the period of great volcanic eruptions must really be attributed to dust veils, it may be presumed that the means of some months have been affected more than those of other months but none sufficiently to mask the pleionian character of the departures. Moreover, the effect of the dust veil ceased long before the complete development of the antipleionian depression of 1904-1905. This antipleion cannot, therefore, be considered as being a consequence of the formation of the volcanic dust veil.

TEMPERATURES AT PARÁ, CAYENNE AND THE WEST INDIES

Although the different examples I have given may be considered as a sufficient proof of the fact that the pleionian variations are absolutely distinct in their origin from the possible temperature variations due to the presence of volcanic dust, I will examine a few more consecutive tem-

⁵⁰ HENRYK ARCTOWSKI: "Notice sur les variations de longue durée des amplitudes moyennes de la marche diurne de la température en Russie." Bull. Soc. belge d'Astronomie. Bruxelles, 1908.

perature curves simply to show how cautious one has to be in the study of the cause of local climatic variations.

In the following diagram (Fig. 5), I reproduce the curves of the consecutive means of temperature for Pará,⁵¹ Cayenne⁵² and the West Indian

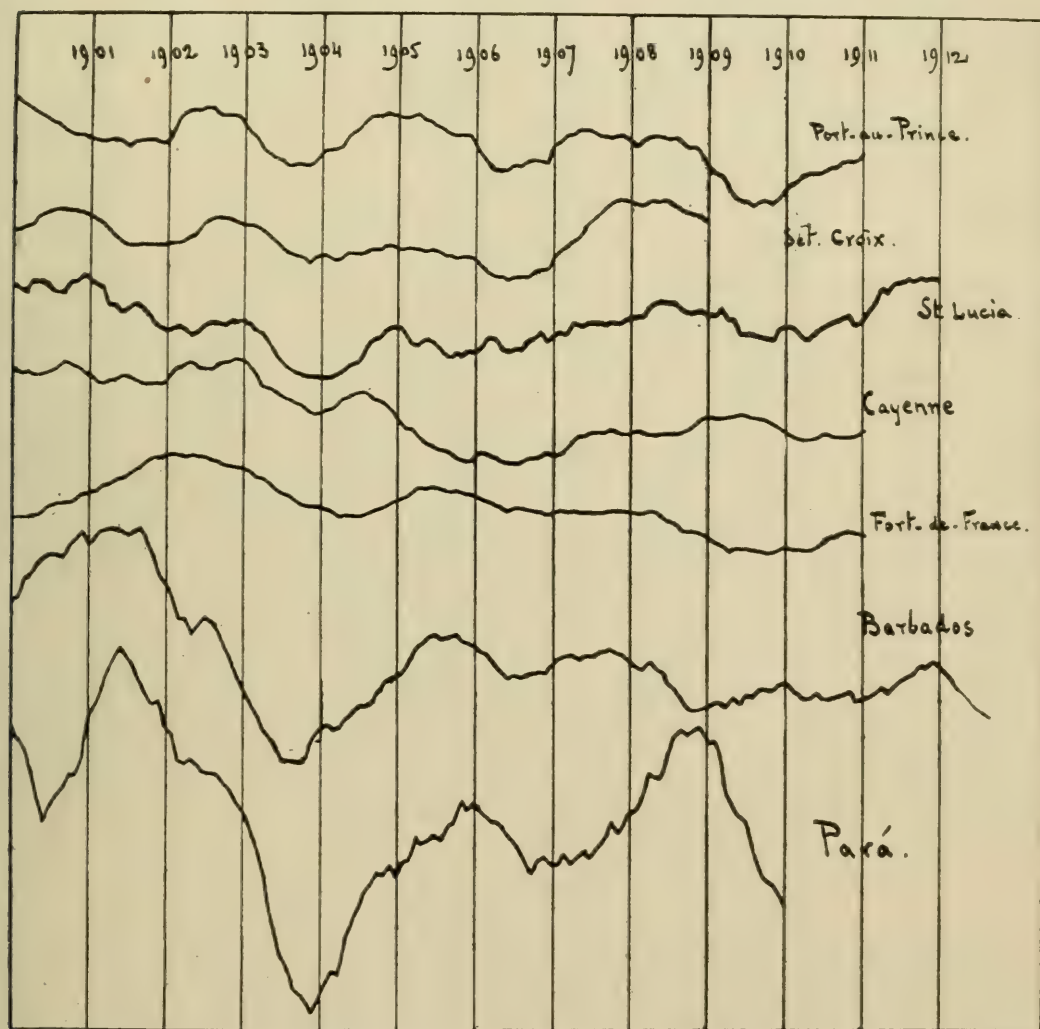


FIG. 5.—Comparison of the consecutive temperature curves of Cayenne and Pará with those of the West Indies

stations: Port-au-Prince,⁵³ St. Croix Christianssted,⁵⁴ St. Lucia and Barbados,⁵⁵ together with the curve of Fort-de-France.

The curves of St. Lucia and Barbados are so very different from the curve of Fort-de-France that one would be inclined to admit some errors

⁵¹ Meteorologische Zeitschrift, vols. 23, 24, 28, 31, pp. 517, 431, 215, 139.

⁵² Annales Bur. Centr. Météorol. de France.

⁵³ Annales Bur. Centr. Météorol. de France.

⁵⁴ Meteorologisk Aarbog for 1900...1909. Udgivet af det danske meteor. Institut.

⁵⁵ Received in manuscript from the Meteorological Office in London.

of observations. But the curve of St. Lucia is a transitional form between those of Fort-de-France and Barbados, and Pará, in Brazil, $1^{\circ} 27'$ S. lat., shows, between 1902 and 1905, exactly the same abnormal depression as Barbados. A very accentuated depression between 1903 and 1904 is also characteristic for Arequipa and Mauritius⁵⁶ as well as St. Helena.⁵⁷ The temperature curve of Apia, Samoa Island, displays the same very pronounced antipleionian depression, corresponding perfectly with that of Barbados. It is difficult, therefore, to avoid the conclusion that the curve of Barbados must be correct and that if it differs very greatly from the curves of the other West Indian stations this fact may simply be considered as an interesting subject for special investigation.

For my present purpose the Barbados curve is a very valuable argument against a possible supposition in favor of the volcanic dust hypothesis. One could imagine that if the Fort-de-France temperature records as well as those of some other stations of the West Indies have not been very much affected by the eruption of Mt. Pelé and the other volcanoes, it may be because the dust veils have been carried into the southern hemisphere, and that there the curves of the stations belonging to the belt of the southern trade-winds show the depression just as much, if not more so, than in the case of the Krakatoa eruption.

The fact that Cayenne, which lies between Pará and Barbados, has a curve resembling those of St. Croix and Port-au-Prince and that these stations belong to the northern trade winds, and the fact that the curve of Barbados is similar to those of the southern stations, show that this explanation of the observed anomaly is inadequate.

TEMPERATURES OBSERVED IN ALASKA

Assuming that the volcanic haze produced by the Katmai eruption of June 6, 1912, must have had the greatest effect on the temperatures recorded in Alaska and in Canada, I will now compare the curves of seven stations in Alaska with the curves of Victoria and Edmonton, Mauritius and Arequipa.

The temperature data for the Alaskan stations were obtained from the United States Weather Bureau, the Arequipa daily observations were sent to me by Professor Edw. C. Pickering and the Mauritius data by Dr. H. R. Mill and by the director of the Mauritius observatory. The observations considered extend over the five years 1909-1913.

Since Mt. Katmai could not have affected the temperature conditions of Arequipa and Mauritius, it is safe to take the curves of these stations

⁵⁶ ARCTOWSKI: *Op. cit.* Bull. Am. Geog. Soc., vol. 44, p. 598.

⁵⁷ ARCTOWSKI: *Op. cit.* Annals N. Y. Acad. Sci., vol. 24, p. 109. 1914.

as a standard. Moreover, in my previous publications I have shown that the consecutive means observed at Arequipa express very well the normal pleionian variation and may serve as a standard in all cases of comparison.

In the accompanying diagram (Fig. 6) the consecutive temperature curves along the Pacific coast are represented, together with the Mauritius and Arequipa curves. The latitudes of Fort Liscum, Sitka, Loring and Victoria are: $61^{\circ} 2'$, $56^{\circ} 50'$, $55^{\circ} 32'$ and $48^{\circ} 26' N$.

The occurrence of the eruption coincided with the pleionian crest of Arequipa. For Arequipa the consecutive mean of July, 1911, to June, 1912, is the highest. From then on the temperature decreases until the consecutive mean of October, 1912,-September, 1913. The same is true at Mauritius; but there the pleionian crest is very different from what it is at Arequipa—it is flat. Since the same may be observed on the curve of Victoria, the apparent depression of the crest of this station cannot be ascribed without hesitation to the effect of the Katmai haze.

The other curves—the Fort Liscum curve in particular—resemble the Arequipa curve so very much that we may admit that at least the depression of the values from the mean of August, 1911,-July, 1912, to the mean of December, 1911,-November, 1912, is due to the effect of volcanic dust. The dotted lines indicate the portions of the pleionian crests which may have been depressed.

The curves of the stations at Nome, Tanana and Fairbanks, situated north of the Alaskan range, do not seem to have been affected, and that of Eagle but slightly. In the case of Edmonton, it is difficult to decide.



FIG. 6.—Arequipa pleion of 1911-1912
observed in Alaska

TEMPERATURE VARIATIONS AT STOCKHOLM AND BATAVIA

In a recent publication,⁵⁸ Axel Wallen gives the curve of the consecutive annual means of temperature observed at Stockholm, for the entire series of observations extending from 1756. A comparison of his curve with the Batavia curve which I published some years ago shows that they are very much alike. The monthly departures of Stockholm⁵⁹ present also many striking analogies with those of Batavia.⁶⁰ It would be worth while to make a more detailed examination.

The variations at Stockholm and Batavia seem to be in perfect harmony: a crest of the Stockholm curve corresponds nearly to each crest of the Batavia curve, and the intervals between corresponding crests are approximately the same. It will be necessary to find many more such similar curves, belonging to far distant stations, before the main conclusion which might be inferred from the comparison of the Batavia and Stockholm curves will have the practical value one might expect.

Batavia being in advance of Stockholm, it is easy to understand that, taking seasonal departures—as Hildebrandsson, Mossman and others have done—correlations between these two stations have to be found. But these correlations will evidently be simply apparent correlations. It is not because a given season of the year is abnormally warm in Batavia, that the following season has to be exceptionally warm in Stockholm and so on; but it is because the same pleionian variation appears with the same regularity in one place as in the other, but slightly retarded, that a seasonal correlation between the two places must exist. The Batavia and Stockholm curves give, therefore, a plausible explanation to the so far unexplained correlations between seasonal departures of distant stations.

Coming back to the volcanic dust problem studied in this paper, it is important to notice that the Stockholm curve seems to be more complete than the Batavia curve. The pleion of 1883, which on the Batavia curve has been greatly reduced by the dust veil effect, is very much better developed on the Stockholm curve. In a similar way some apparent anomalies on the Batavia curve may be considered as being really anomalies which would not exist if the curve were perfectly developed as it ought to be. For example, the portion of the consecutive temperature curve of Batavia from 1871 to 1873 is abnormal. Likewise, the long

⁵⁸ AXEL WALLEN: "Fleråriga variationer hos vattenståndet i Mälaren...", *Meddelanden från Hydrografiska Byrån*: 4. Stockholm, 1913.

⁵⁹ H. E. HAMBERG: "Moyennes mensuelles et annuelles de la temperature... à l'observatoire de Stockholm," *Konigl. Svenska Vetenskaps-acad. Handlingar*, vol. 40, no. 1. Stockholm, 1906.

⁶⁰ Observations made at the Royal Magnetical and Meteorological Observatory at Batavia. Vol. 28, p. 108. 1907.

interval between the pleionian crests of 1891 and 1897 of the Batavia curve is due to a missing crest which is well marked on the Stockholm curve.

SUN-SPOTS AND ATMOSPHERIC TEMPERATURE

The conclusion so far is that the thermopleionian variations cannot be ascribed to more or less frequent reoccurrences of volcanic dust veils. In exceptional cases, such as the Krakatoa eruption, atmospheric temperature has been affected practically all over the world; but even then the pleionian crests of the consecutive yearly temperature curves have simply been partially erased, or modified in such a way that there can be no doubt that the antipleionian depressions which followed were not due to the presence of volcanic haze.

The hypothesis that the pleionian variations of temperature have an extra-terrestrial cause is therefore a perfectly logical conclusion.

In order to prove that this hypothesis is well founded, it will be necessary to demonstrate the existence of a correlation between atmospheric temperature and solar radiation, or perhaps some other phenomenon of which the "solar constant" is a function.

It has been presumed that differences in the extent or relative position of the Zodiacal light might be such a phenomenon.⁶¹ Variations of the solar corona could possibly also have some effect on the radiant energy transmitted towards the earth;⁶² but it seems more probable that atmospheric temperature is directly affected by changes occurring on the sun's surface or solar atmosphere.⁶³ The well known sun-spot cycle of about 11 years' mean duration proves it very well.

It was Alfred Gautier⁶⁴ who, as far back as 1844, discovered the relation that exists between atmospheric temperature and the solar cycle.

⁶¹ E. BELOT: "La matière zodiacale et la constante solaire," C. R. Ac. Sci. Paris, vol. 157, p. 757. 1913.

⁶² A. CROVA: "Etude de l'intensité calorifique de la radiation solaire au moyen de l'actinomètre enregistreur," Annales de chimie...ser. 6, vol. 14, p. 543. Paris, 1888.

Some arguments in favor of this hypothesis may also be found in the following papers:

S. P. LANGLEY: "The Heat Radiation of the Corona," Astroph. Journal, vol. 12, p. 371. 1900.

C. G. ABBOT: "A Bolometric Study of the Solar Corona," Publ. Astron. Soc. Pacific, vol. 20, p. 86. 1908.

JOHN A. MILLER: "The Position of Certain Coronal Streams on the Assumption that the Corona is a Mechanical Product," Astroph. Jour., vol. 33, p. 303. 1911.

⁶³ S. P. LANGLEY: "The Solar Atmosphere, an Introduction to an Account of Researches made at the Allegheny Observatory," Amer. Jour. Sci., ser. 3, vol. 10, p. 489. 1875.

J. HAHN: "Contributions to the Theory of the Sun," Annals Roy. Obs. Edinburgh, vol. 1, p. 74. 1902.

⁶⁴ ALFRED GAUTIER: "Recherches relatives à l'influence que le nombre et la permanence des taches observées sur le disque du soleil peuvent exercer sur les températures terrestres," Annales de chim. et de phys., ser. 3, vol. 12, p. 57. 1844.

Since then many researches have been made. A recent publication by W. Koeppen⁶⁵ gives the most convincing data. Koeppen utilized the annual temperature means collected by J. Mielke,⁶⁶ as well as the figures which served him in previous publications on this subject, and completed the tables in order to have the results of practically all available observations made, all over the world, from 1811 to 1910. The final result may be advantageously reproduced in a form slightly different from that given by Koeppen.⁶⁷

The following figures represent the mean departures from the general means for the years of sun-spot maxima and of those before and after these years:

-3	-2	-1	⊙ Max.	+1	+2	+3 years
+0.09	-0.03	-0.15	-0.23	-0.15	-0.15	+0.07 °C.

The means of the years of sun-spot minima, as well as the means of the years preceding and following these minima, are given below:

-3	-2	-1	⊙ Min.	+1	+2	+3 years
-0.11	+0.07	+0.24	+0.22	+0.11	+0.04	0.00 °C.

The conclusion is that the solar cycle of about 11 years' mean duration has a well pronounced influence upon atmospheric temperature, and that the difference between maxima and minima equals on the average nearly 0.5 °C.

But the diagram representing the succession of the preceding figures graphically shows that the 11-year period is complicated by the existence of a shorter variation of less importance. It seems that during the sun-spot cycle, temperature undergoes a double oscillation; that between the consecutive temperature minima, corresponding to sun-spot maxima, there are two minima and three maxima, one of which corresponds to the sun-spot minimum. The diagram given by Koeppen for the Russian temperature data is perhaps the best illustration of this fact.

⁶⁵ W. KOEPPEN: "Lufttemperaturen, Sonnenflecke und Vulkanausbrüche," Meteor. Zeitsch., vol. 31, p. 305. 1914.

⁶⁶ JOHANNES MIELKE: "Die Temperaturschwankungen 1870-1910 in ihrem Verhältnis zu der 11 jährigen Sonnenfleckenperiode," Aus dem Archiv der deutschen Seewarte, vol. 36, no. 3. 1913.

⁶⁷ Koeppen adds the annual temperature departures of the years of sun-spot minimum, one year after, two a. s. f. This gives him 11 columns of figures. The disadvantage of this method is that the year of sun-spot maximum occurs once in column 4, 3 times in column 5, 4 times in column 6 and once in column 9. His first column of figures comprises the departures for the years 1811, 1822, 1833, 1844, 1855, 1867, 1878, 1889 and 1900. Only four of these years are years of sun-spot minima; the others precede or follow such a year. However it would have been difficult to make a better adjustment than Koeppen did.

In the case of rainfall, Charles Meldrum⁶⁸ long ago noticed the double oscillation. For the weather conditions in the United States, Frank H. Bigelow⁶⁹ found that "the occurrence of four subordinate crests in the 11-year periods suggests strongly that a $2\frac{3}{4}$ -year period is superposed upon the long sweep of that periodic curve." Later, Bigelow⁷⁰ discovered a correlation between this short period variation and the frequency changes of solar prominences.

One may conclude that Koeppen's calculations give only a first approximation, and that in reality the phenomenon of the 11 years' variation is complicated by a variation of a shorter periodicity, perhaps also in connection with the changes of sun-spot frequency.

A strong argument in favor of this supposition is the circumstance that the commonly known 11 years' variation is not the only sun-spot cycle. The relative numbers of Wolf and Wolfer have been analyzed by Arthur Schuster,⁷¹ who found the following periods: 13.5, 11.125, 8.36, 5.56, 4.79, 3.71. Hisashi Kimura,⁷² on the other hand, found periods of 16.59, 13.53, 11.114, 9.99, 8.25, 5.95, 5.49, 4.85 and 3.63 years. According to the most recent investigations⁷³ it may be, however, that, "while these various periods are apparent, yet many are illusory."

All these researches show very plainly that the frequency variation of sun-spots is a most complicated phenomenon. So are also the temperature variations. It is certain that the pleionian variation of the Arequipa or equatorial type has apparently nothing in common with the 11-year cycle; but some correlations exist. In 1893 the antipleions were predominant. The year 1900 was a pleionian year. One may presume, therefore, that the solar cycle of 11 years has a direct influence on the long range or macropleionian variations and that the shorter pleionian and antipleionian oscillations of terrestrial temperature are the product of some minor sun-spot cycle, or perhaps of some other solar cycle which does manifest itself with the same evidence as the sun-spot frequency variations.

As soon as the particulars of the pleionian variations are better known,

⁶⁸ CHARLES MELDRUM: "Report on Sun-spots and Rainfall," Rep. 48th meeting Brit. Assoc., p. 257. 1879.

⁶⁹ FRANK H. BIGELOW: "Abstract of a Report on Solar and Terrestrial Magnetism in their Relations to Meteorology," Bull. no. 21, U. S. Weather Bur., p. 125. 1898.

⁷⁰ FRANK H. BIGELOW: "The Relations Between the Meteorological Elements of the United States and the Solar Radiation," Amer. Jour. Sci., ser. 4, vol. 25, p. 423. 1908.

⁷¹ ARTHUR SCHUSTER: "On the Periodicities of Sun-spots," Phil. Trans. Roy. Soc. London, vol. 206 A., p. 69. 1906.

⁷² HISASHI KIMURA: "On the Harmonic Analysis of Sun-spot Relative Numbers," Monthly notices Roy. Astr. Soc., vol. 73, p. 543. 1913.

⁷³ A. E. DOUGLASS: "A Photographic Periodogram of the Sun-spot Numbers," Astroph. Jour., vol. 40, p. 326. 1914.

it will be possible to reverse the problem and search in the variable solar phenomena for the periodicities which might correspond to the changes of atmospheric temperature. But the problem is extremely complicated. All we know about climatic variations is derived from observations taken at the earth's surface. Now, Charles J. Kullmer⁷⁴ "has shown that in the belt of the northern United States and southern Canada where storms on the average are most numerous, the number of storms varies almost directly in harmony with the number of sun-spots, just as is the case with tropical hurricanes. In other areas, however, the reverse appears to be true, and there is a decrease in storminess. The general conclusion seems to be that when sun-spots are few in number cyclonic storms move in a great variety of tracks, but when spots are numerous the storms tend to confine themselves to a few well-defined tracks, so that storminess is more or less restricted to certain areas within which it is highly concentrated."⁷⁵ If we bear in mind the fact that storms are centered by columns of ascending air, we must presume that on the average differences in storm frequency (and intensity) must produce corresponding differences in the vertical distribution of temperature. Ellsworth Huntington supposes that "in this way increased activity of the sun might cause increased activity upon the earth, and the earth's surface might become cooler while the upper air above the reach of convection might become warmer."⁷⁶ This most interesting suggestion could be verified, I suppose.

Utilizing the table of Leo Kelley, giving the annual frequencies of eruptions,⁷⁷ as well as Koeppen's world's mean temperature table, I made for both overlapping ten-yearly totals. The following diagram (Fig. 7) represents the figures graphically and shows plainly that some sort of a relation between the numbers of volcanic eruptions and atmospheric temperature is undeniable.

Temperature seems to be higher when the eruptions are more frequent and when volcanic activity is attenuated, atmospheric temperature seems also to be lower than the average. This result is not in favor of the volcanic dust explanation of climatic variations and if taken in connection with the remarkable coincidences between the well pronounced

⁷⁴ CHARLES J. KULLMER: "The Shift of the Storm Track," In: E. Huntington: "The Climatic Factor..." p. 193. Carnegie Inst. Pub. No. 192. 1904.

⁷⁵ ELLSWORTH HUNTINGTON: *Op. cit.*, p. 253.

⁷⁶ Manuscript communication. Huntington discusses the question at length in his recent paper, "The Solar Hypothesis of Climatic Changes," Bull. Geol. Soc. Amer., vol. 25, p. 477. 1914.

⁷⁷ JOHN MILNE: "Eighteenth Report of the Committee on Seismological Investigations," p. 65. Report of the 83rd meeting of the Brit. Assoc. Birmingham. 1913.

pleions of the years 1883, 1902 and 1912 and the exceptionally violent volcanic eruptions which occurred simultaneously, shows that it may be that the volcanic agencies are affected by the same extra-terrestrial factors which influence climatic conditions.

How this could be, is a most interesting question leading to many investigations. One may presume, for example, some correlations between the pleionian variation and storm frequency and storm intensity

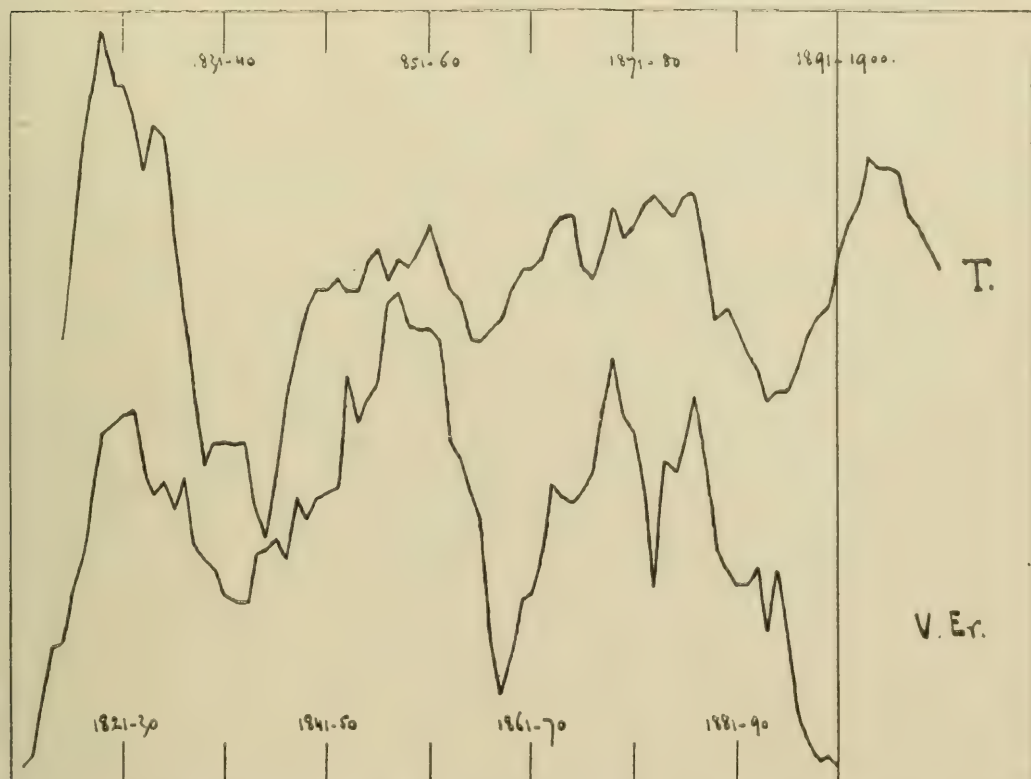


FIG. 7.—World's temperature and the variation of the frequency of volcanic eruptions

and then a correlation between the more or less accentuated rapid oscillations of atmospheric pressure and volcanic eruptions.

A relationship between the mean values of interdiurnal differences of atmospheric pressure and the solar cycle has been discovered by R. Merecki,⁷⁸ and, on the other hand, the much discussed relation between barometric changes from day to day, and the frequency of seismic and volcanic phenomena may be accepted as an established fact.⁷⁹ One may

⁷⁸ R. MERECKI: "Wpływ zmiennej działalności słońca na czynniki meteorologiczne ziemskie," *Prace mat.-fizyczne*, vol. 19, p. 131. Warszawa, 1908.

⁷⁹ F. OMORI: "Note on the Long-period Variations of the Atmospheric Pressure," *Bull. Imp. Earthq. Invest. Comm.*, vol. 2, p. 215. Tokyo, 1908.

H. J. JOHNSTON-LAVIS: "The Relationship of the Activity of Vesuvius to Certain Meteorological and Astronomical Phenomena," *Proc. Roy. Soc. London*, vol. 40, p. 248. 1886.

ask, therefore, if the amplitudes of the barometric oscillations vary in harmony with the pleionian cycles.

CONCLUSIONS

1). The hypothesis attributing most climatic variations to volcanic dust veils, although verified in some cases, presents more a purely theoretical than practical interest.

2). The dust veil produced by the Krakatoa eruption affected atmospheric temperature very greatly. The violent volcanic eruptions of 1902, as well as the Katmai eruption of 1912, influenced the yearly mean temperatures but very slightly or not at all.

3). The pleionian variations of temperature have nothing in common with the presence or absence of volcanic dust veils.

4). An influence of the sun-spot variation upon the changes of atmospheric temperature is undeniable.

5). In some exceptional cases, at far-distant stations, such close correspondences of the pleionian variations may be observed that one is justified in admitting that missing crests are due to locally restricted anomalies. Of course, in most cases the anomalies are prevalent.

6). A correlation between pleionian and macropleionian temperature variations and the occurrence and frequency of volcanic eruptions may be presumed, although, at present, it is difficult to imagine how such a correlation could be explained.

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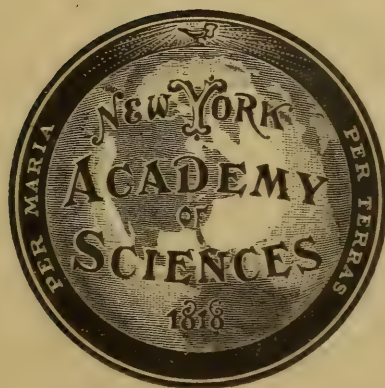
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STATISTICAL STUDY OF VARIATION IN
SPIRIFER MUCRONATUS

BY

CHARLES C. MOOK



NEW YORK
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STATISTICAL STUDY OF VARIATION IN SPIRIFER MUCRONATUS¹

BY CHARLES C. MOOK

(Presented in abstract before the Academy, 7 December, 1914)

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INTRODUCTION

These studies were made on specimens of five mutations of *Spirifer mucronatus* collected by Professor A. W. Grabau and Dr. H. W. Shimer near Thedford, Ontario, and by Professor Grabau near Alpena and at other localities in Michigan.

The beds from which these fossils were collected correspond, in whole or in part, with the Hamilton of New York State. The general succession of beds in the Michigan region is given below. At the base are calcareous shales corresponding in a general way with the lower part of the Hamilton or upper part of the Marcellus of the New York State section. These shales contain the mutation of *Spirifer mucronatus* called by Grabau *alpenense*. Above these shales there is a series of alternating limestones and calcareous shales. The limestones contain the mutation *multiplicatus* and the shales contain the mutation *alpenense*. Above this series there is another series of calcareous shales containing the mutations *profundus* and *attenuatus*. In the Thedford section, the mutation *thedfordense* Shimer and Grabau occurs in shales corresponding approximately with those containing *profundus* and *attenuatus* in Michigan.

The objects of the studies were to determine, if possible, the relations of the different mutations to each other, the progress of evolution in the

¹ Manuscript received by the Editor 16 December, 1914.

various lines, and to make a trial of the statistical method in the study of fossils.

The curves were made by plotting the percentages of the total number of individuals having indices between certain prescribed limits. The indices were taken as abscissæ and the percentages as ordinates. The higher indices were indicated on the right and the lower on the left. Progression has been indicated as going from right to left.

The mutation *thedfordense* was described by Shimer and Grabau in 1902.² Descriptions of the other mutations are taken to a large extent from Grabau manuscript.

MUTATION I.—*Spirifer mucronatus* MUT. *alpenense* GRABAU MS.

This mutation occurs in the lowest beds of the Michigan Hamilton in a shaly matrix. It is of moderate size, with fairly strong growth lines. The plications are close together and are not very strong. They number about fifteen on each side of the fold and sinus. The shell is sometimes extended into a pair of mucronate wings. The sinus is broad and shallow and contains no median plication. The fold is also broad and shallow, and sometimes contains a median groove in the *young stages*. There is never a median groove on the fold of the adult. Three hundred and seventy-two individuals of this mutation were measured and the following is a summary of the results. The complete measurements are given in the tables.

Maximum width.....	42mm.
Minimum width.....	15
Maximum length.....	28
Minimum length.....	9
Maximum shell index (adult).....	2.80
Minimum shell index (adult).....	.95
Average shell index (adult)..... (about) ..	1.50
Maximum shell index (neanic stage).....	4.30
Minimum shell index (neanic stage).....	1.29
Average shell index (neanic stage)..... (about) ..	2.60

TABLE I.—Number of individuals and percentages of total number of individuals of various indices

Index	Adult		Neanic	
	Number	Percentage	Number	Percentage
-1.00	3	.8	0	0
1.01-1.25	63	16.9	0	0
1.26-1.50	111	29.8	1	.2
1.51-1.75	107	28.7	15	4.0
1.76-2.00	57	15.3	51	13.6

² Bull. Geol. Soc. Am., vol. 13, pp. 149-153.

Index	Adult		Neanic	
	Number	Percentage	Number	Percentage
2.01-2.25	23	6.1	62	16.6
2.26-2.50	5	1.3	69	18.5
2.51-2.75	2	.5	60	16.1
2.76-3.00	1	.2	45	12.0
3.01-3.25	0	0	26	6.9
3.26-3.50	0	0	21	5.6
3.51-3.75	0	0	15	4.0
3.76-4.00	0	0	4	1.0
4.01-4.25	0	0	2	.5
4.26-4.50	0	0	1	.2
Total.....	372	99.6	372	99.2

The curve of the adult shell indices of *alpenense* is fairly smooth. The slight roughness or irregularity may be attributed to imperfection of some of the specimens and to the difficulty of deciding, in some cases, the anterior end of the pedicle valve. The neanic curve is much more irregular, a condition due, no doubt, to the extreme difficulty of finding exactly corresponding growth stages in a great number of individuals.

From the size, characters and number of plications, shell indices and characters of the fold and sinus, *alpenense* is favorably equipped to be an ancestor of the mutations *profundus* and *thedfordense*.

MUTATION II.—*Spirifer mucronatus* MUT. *multiplicatus* GRABAU MS.

This mutation occurs in the limestone beds in the Michigan region above the shales containing *alpenense*. Shales bearing *alpenense* sometimes alternate with these limestones. It is a large mutation with many fairly strong flat plications. There are about 17 plications on each side of the fold and sinus. The fold and sinus are broad and flat, the sinus bearing a well-developed plication and the fold a median groove. The growth lines are strong and the young stages are often clearly distinguishable. Twenty-nine individuals of *multiplicatus* were measured.

Maximum width.....	50mm.
Minimum width.....	26
Maximum length.....	27
Minimum length.....	15
Highest shell index (adult).....	2.32
Lowest shell index (adult).....	1.46
Average shell index (adult)..... (about) ..	1.80
Highest shell index (neanic stage).....	3.50
Lowest shell index (neanic stage).....	1.78
Average shell index (neanic stage)..... (about) ..	2.65

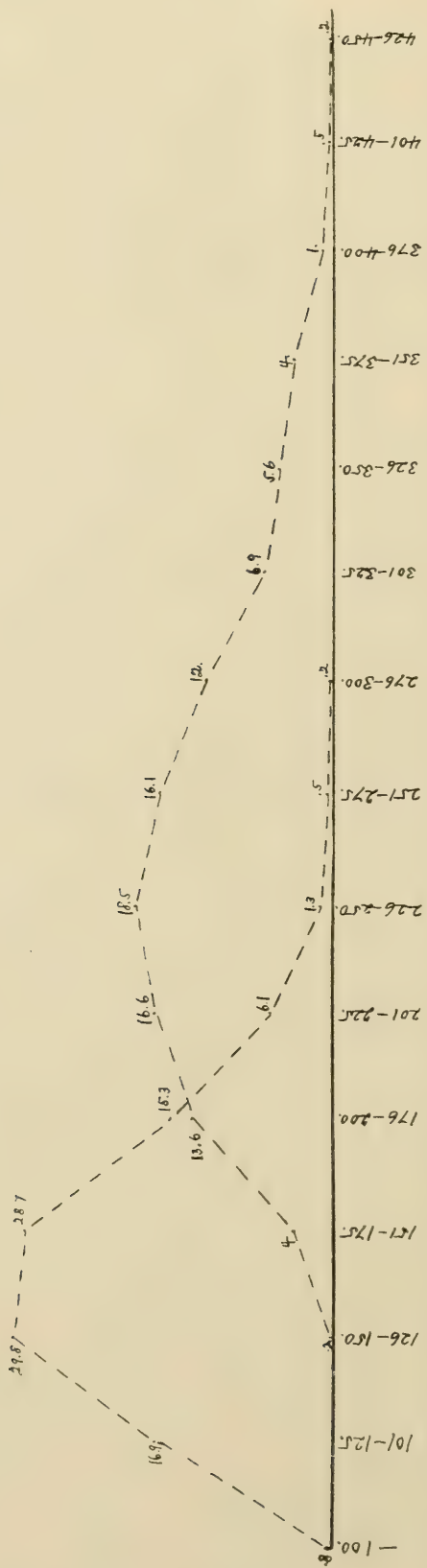


FIG. 1.—Curves showing comparative conditions of shell indices in adult and neanic stages of *Spirifer mucronatus mut. alpenense*

TABLE II.—Number of individuals and percentages of total number of individuals of various indices

Index	Adult		Neanic	
	Number	Percentage	Number	Percentage
1.26-1.50	3	10.3	0	0
1.51-1.75	11	37.9	0	0
1.76-2.00	9	31	2	6.8
2.01-2.25	5	17.2	5	17.2
2.26-2.50	1	3.4	6	20.6
2.51-2.75	0	0	10	34.4
2.76-3.00	0	0	2	6.8
3.01-3.25	0	0	3	10.3
3.26-3.50	0	0	1	3.4
Total.....	29	99.8	29	99.5

The adult curve of *multiplicatus* is narrow and regular. The neanic curve is broad and very irregular.

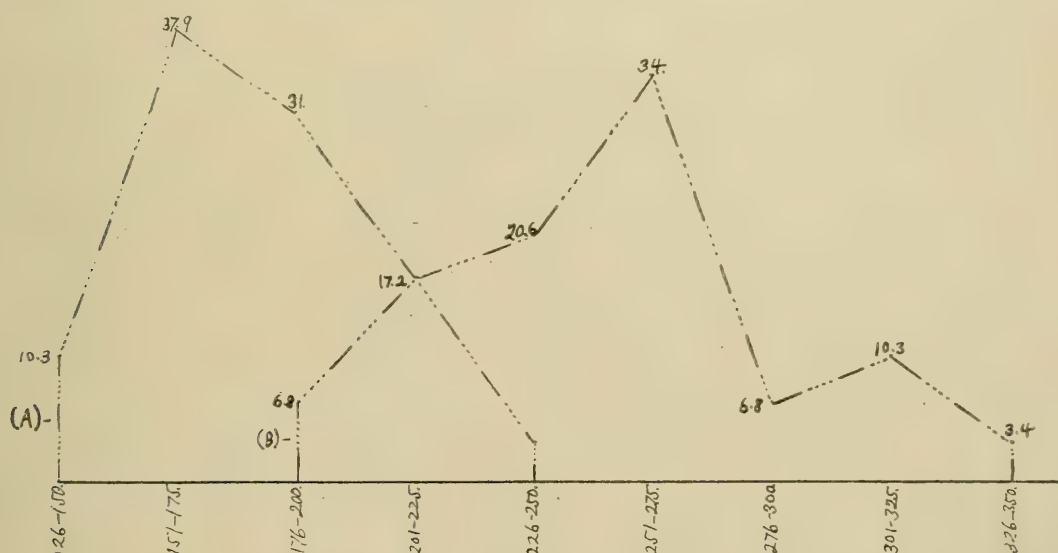


FIG. 2.—Curves showing comparative conditions of shell indices in adult and neanic stages of *Spirifer mucronatus* mut. *multiplicatus*

MUTATION III.—*Spirifer mucronatus* MUT. *profundus* GRABAU MS.

This mutation occurs with *attenuatus* in the upper shales in the Michigan region. It is small with extremities not at all or only slightly mucronate. The median sinus is deep and angular. It extends from the beak to the anterior end, then beyond into the brachial valve. The bottom of the sinus is subangular. The fold on the brachial valve is shallow and has no median depression. The plications are round and close together. There are 8 to 12 on each side of the fold or sinus,

rarely less. The growth lines are strongly turned back over the fold and sinus.

Maximum width.....	35mm.
Minimum width.....	15
Maximum length.....	21
Minimum length.....	9
Highest shell index (adult).....	2.71
Lowest shell index (adult).....	.97
Average shell index (adult).....(about) ..	1.65
Highest shell index (neanic stage).....	4.37
Lowest shell index (neanic stage).....	1.35
Average shell index (neanic stage).....(about) ..	2.50

The adult curve is fairly short and regular. It corresponds closely with the adult curve of *alpenense*, though the average index is a little lower. The neanic curve is very broad and irregular. It corresponds rather closely with the neanic curve of *alpenense*. The average neanic index, however, is a little lower. Two hundred and seventy-six individuals were measured.

TABLE III.—*Number of individuals and percentages of total number of individuals of various indices*

Index	Adult		Neanic	
	Number	Percentage	Number	Percentage
-1.00	2	.7	0	0
1.01-1.25	36	13.0	0	0
1.26-1.50	112	40.5	2	.7
1.51-1.75	75	27.1	6	2.1
1.76-2.00	40	14.4	37	13.4
2.01-2.25	6	2.1	72	26.0
2.26-2.50	3	1.0	52	18.8
2.51-2.75	2	.7	60	21.5
2.76-3.00	0	0	31	11.2
3.01-3.25	0	0	8	2.8
3.26-3.50	0	0	4	1.4
3.51-3.75	0	0	0	0
3.76-4.00	0	0	2	.7
4.01-4.25	0	0	1	.35
4.26-4.50	0	0	1	.35
Total.....	276	99.5	276	99.3

This mutation is evidently an offshoot from the *alpenense* stem. The line of development has been more in the nature of a deepening of the sinus and strengthening of the growth lines rather than in reducing the shell index. The shell index is a little lower than that of *alpenense* in

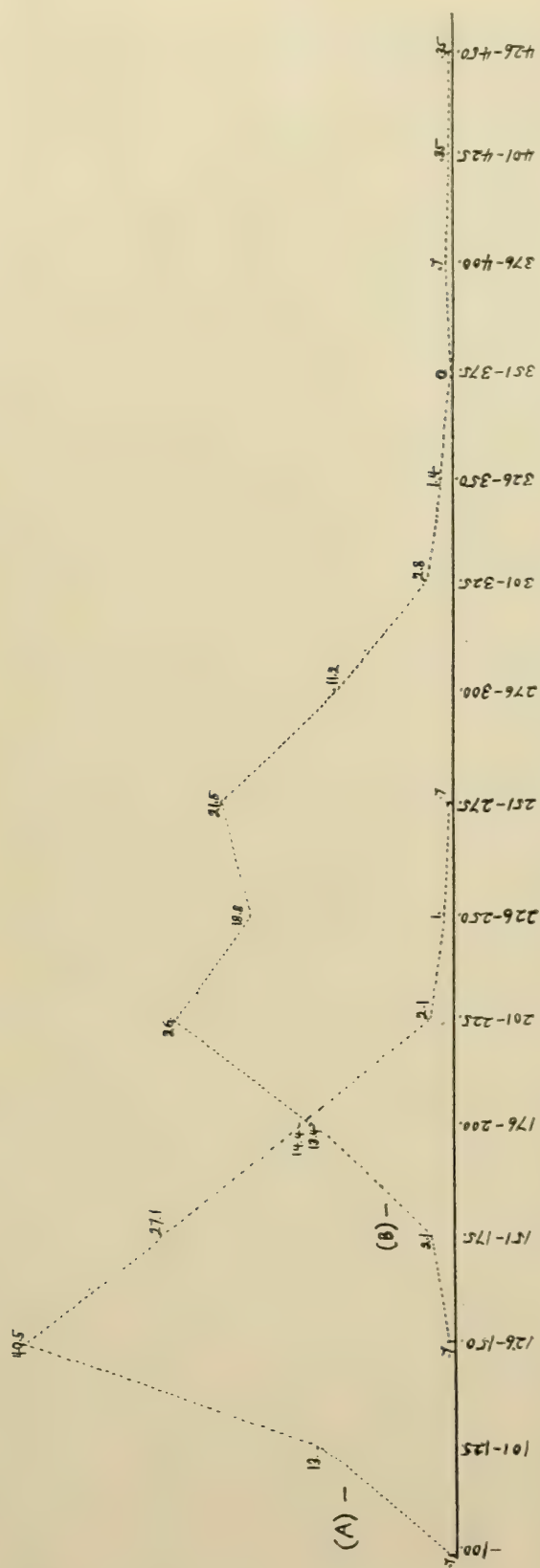


FIG. 3.—Curves showing comparative conditions of shell indices in adult and neanic stages of *Spirifer mucronatus mut. profundus*

the adult stage, but only a mere trifle lower in the neanic stage. This in itself is an indication of progression toward a low indexed condition.

MUTATION IV.—*Spirifer mucronatus* MUT. *thedfordense* SHIMER AND GRABAU

The mutation *thedfordense* occurs in the upper Hamilton shales in the region about Thedford, Ontario.

This mutation is the most advanced of the five mutations studied. It is fairly good-sized and very stout. There are 12 to 15 strong sharp plications on each side of the fold and sinus. The sinus is deep and subangular in the adult and occasionally has a faint elevation in the very young stages. The fold is somewhat elevated and rounded in the adult, and often shows a faint median depression in the young stages. The growth lines are very prominent, and are sharply deflected over the fold, sinus, and plications. Two hundred and thirty-one individuals were measured.

Maximum width.....	45mm.
Minimum width.....	23
Maximum length.....	35
Minimum length.....	15
Highest shell index (adult).....	1.94
Lowest shell index (adult).....	.89
Average shell index (adult)..... (about) ..	1.30
Highest shell index (neanic stage).....	3.56
Lowest shell index (neanic stage).....	1.24
Average shell index (neanic stage)..... (about) ..	2.00

TABLE IV.—Number of individuals and percentages of total number of individuals of various indices

Index	Adult		Neanic	
	Number	Percentage	Number	Percentage
-1.00	24	10.3	0	0
1.01-1.25	107	46.3	2	.8
1.26-1.50	80	34.6	17	7.3
1.51-1.75	15	6.4	54	23.3
1.76-2.00	5	2.1	63	26.8
2.01-2.25	0	0	40	17.3
2.26-2.50	0	0	24	10.3
2.51-2.75	0	0	18	7.7
2.76-3.00	0	0	10	4.3
3.01-3.25	0	0	1	.4
3.26-3.50	0	0	1	.4
3.51-3.75	0	0	1	.4
Total.....	231	99.7	231	99.0

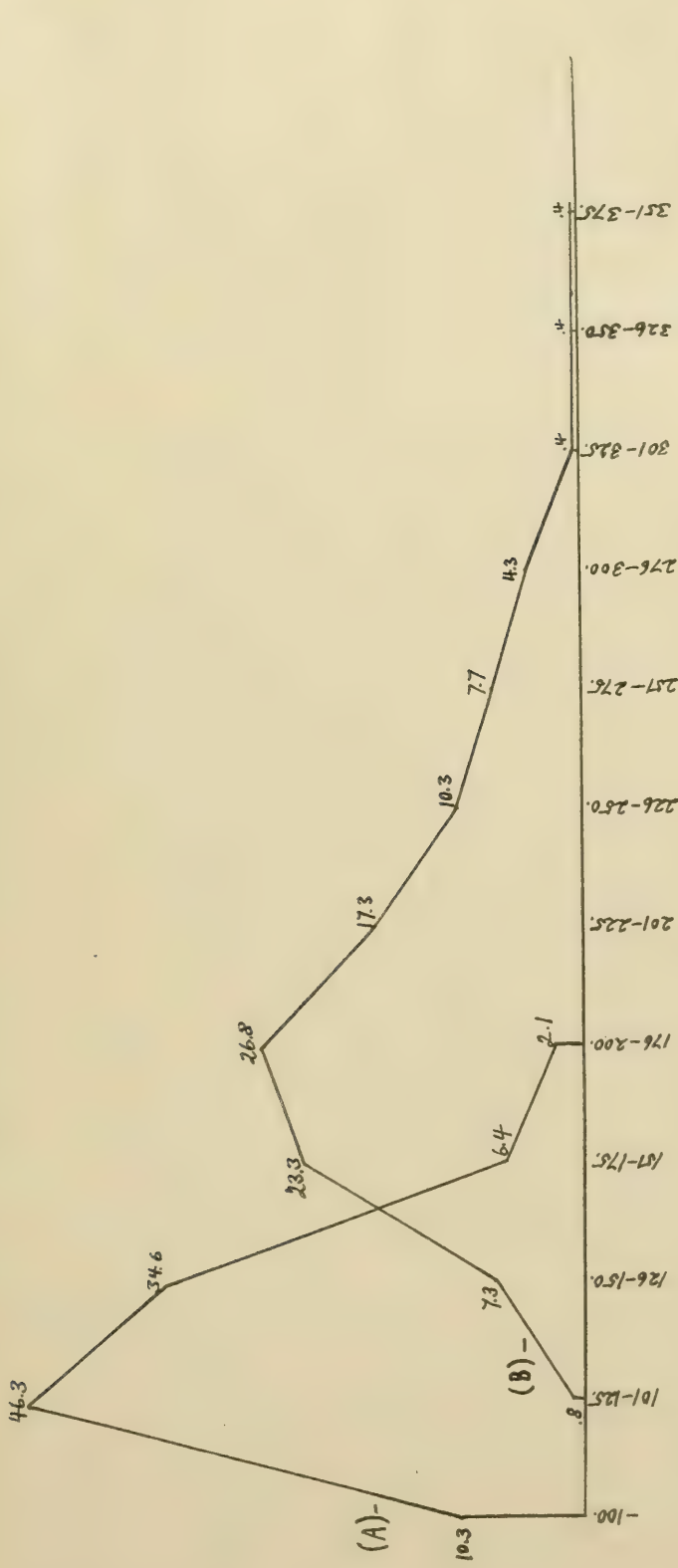


FIG. 4.—Curves showing comparative conditions of shell indices in adult and neanic stages of *Spirifer mucronatus* mut. thedordense

The adult curve is very narrow considering the large number of individuals measured. It is regular in form. The neanic curve is fairly regular and is very wide. It would correspond fairly well with a flattened-out curve of the adult.

Thedfordense was evidently derived from *alpenense* along with *profundus*. It differs from *profundus* in having vestiges of a plication in the sinus and groove in the fold, in being more robust, and in having a lower shell index. *Profundus* has progressed further in the deepening of the fold and sinus, and *thedfordense* further in reduction of the shell index.

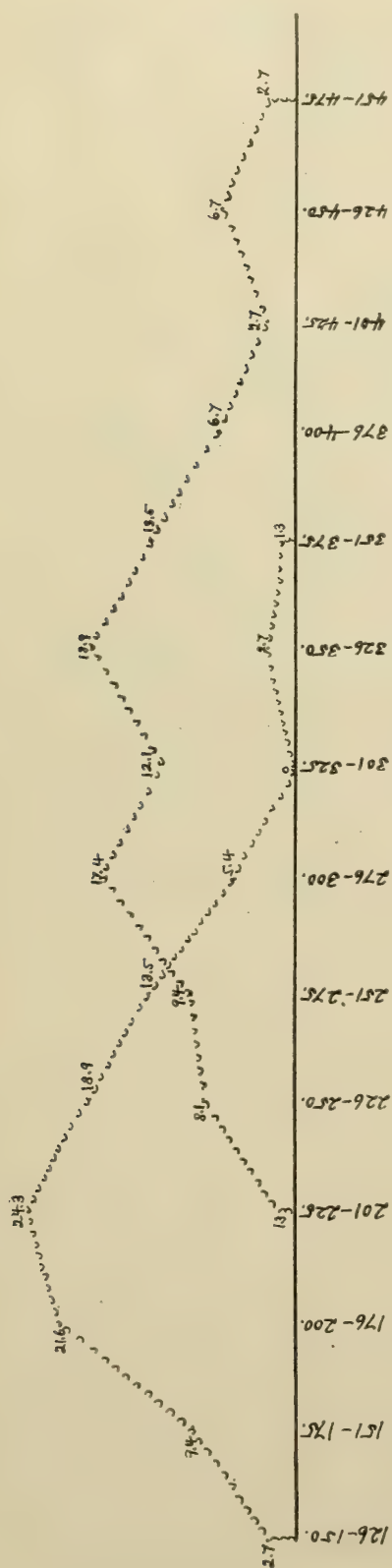
MUTATION V.—*Spirifer mucronatus* MUT. *attenuatus* GRABAU MS.

Attenuatus occurs in the upper shales in the Michigan region along with *profundus*. The shell is very wide and short, giving a high shell index. The sinus of the pedicle valve has a distinct median plication which extends nearly to the beak. The fold of the brachial valve is flat and level with the plications on either side or slightly elevated above them. It has a pronounced median groove which extends nearly to the beak. The growth lines are moderately strong. There are 15 to 18 strong plications on each side of the fold and sinus.

Maximum width.....	47mm.
Minimum width.....	19
Maximum length.....	17.5
Minimum length.....	8
Highest shell index (adult).....	3.75
Lowest shell index (adult).....	1.37
Average shell index (adult)..... (about) ..	2.25
Highest shell index (neanic stage).....	4.70
Lowest shell index (neanic stage).....	2.23
Average shell index (neanic stage)..... (about) ..	3.40

TABLE V.—Number of individuals and percentages of total number of individuals of various indices

Index	Adult		Neanic	
	Number	Percentage	Number	Percentage
1.26-1.50	2	2.7	0	0
1.51-1.75	7	9.4	0	0
1.76-2.00	16	21.6	0	0
2.01-2.25	18	24.3	1	1.3
2.26-2.50	14	18.9	6	8.1
2.51-2.75	10	13.5	7	9.4
2.76-3.00	4	5.4	13	17.6
3.01-3.25	0	0	9	12.1
3.26-3.50	2	2.7	14	18.9

FIG. 5.—Curves showing comparative conditions of shell indices in adult and neanic stages of *Spirifer mucronatus mut. attenuatus*

Index	Adult		Neanic	
	Number	Percentage	Number	Percentage
3.51-3.75	1	1.3	10	13.5
3.76-4.00	0	0	5	6.7
4.01-4.25	0	0	2	2.7
4.26-4.50	0	0	5	6.7
4.51-4.75	0	0	2	2.7
Total.....	74	99.8	74	99.7

The adult curve of *attenuatus* is broad and rather irregular. The neanic curve is very broad and irregular.

This mutation is in many respects the most primitive of the five mutations studied, although it occurs in the highest of the three horizons. It is nearest to *multiplicatus* in form and general characters though *multiplicatus* has a lower shell index.

The derivation of *attenuatus* is uncertain, though it is not far removed from *multiplicatus*. Several possibilities may be considered. *Attenuatus* may be derived from some form of *multiplicatus* whose index is much higher than any of those measured. It may have come from a *multiplicatus* stock having an index like the highest of those measured and then degenerated into a short and broad form. It may have sprung from a common ancestor with *multiplicatus* in a lower horizon and remained primitive while *multiplicatus* progressed toward a lower index. The third possibility is by far the most probable. The adult curve of *attenuatus* corresponds roughly with the neanic curve of *multiplicatus*.

CONCLUSION

Two distinct lines of development have been observed in *Spirifer mucronatus*. In one of these lines development has advanced to a considerable distance from the primitive *Spirifer mucronatus* condition. This line includes *alpenense*, *profundus*, and *thedfordense*. The other line has progressed much more slowly. This line contains *multiplicatus* and *attenuatus*. In the first line *thedfordense* and *profundus* have probably been derived directly from *alpenense*. In the second line *attenuatus* was probably not derived directly from *multiplicatus*, but from a form closely resembling *multiplicatus*, but more primitive. *Multiplicatus* and *alpenense* were probably derived from some primitive form of *Spirifer mucronatus* belonging to a lower horizon than any of the five mutations studied. The approximate relations of the five mutations to each other are shown graphically in the following diagram.

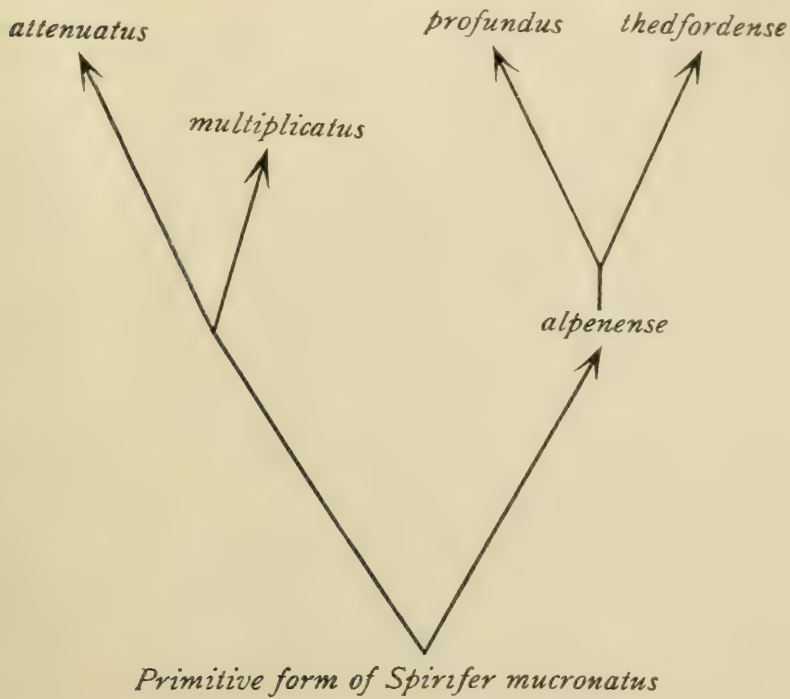


FIG. 6.—Diagram showing the relationships of the five mutations of *Spirifer mucronatus*

The tendency in development has been to reduce the shell index, to reduce the number of plications, to lose the groove and plication on fold and sinus, to strengthen the growth lines and individual plications, to deepen the sinus, and to a certain extent to reduce the actual width of the shell.

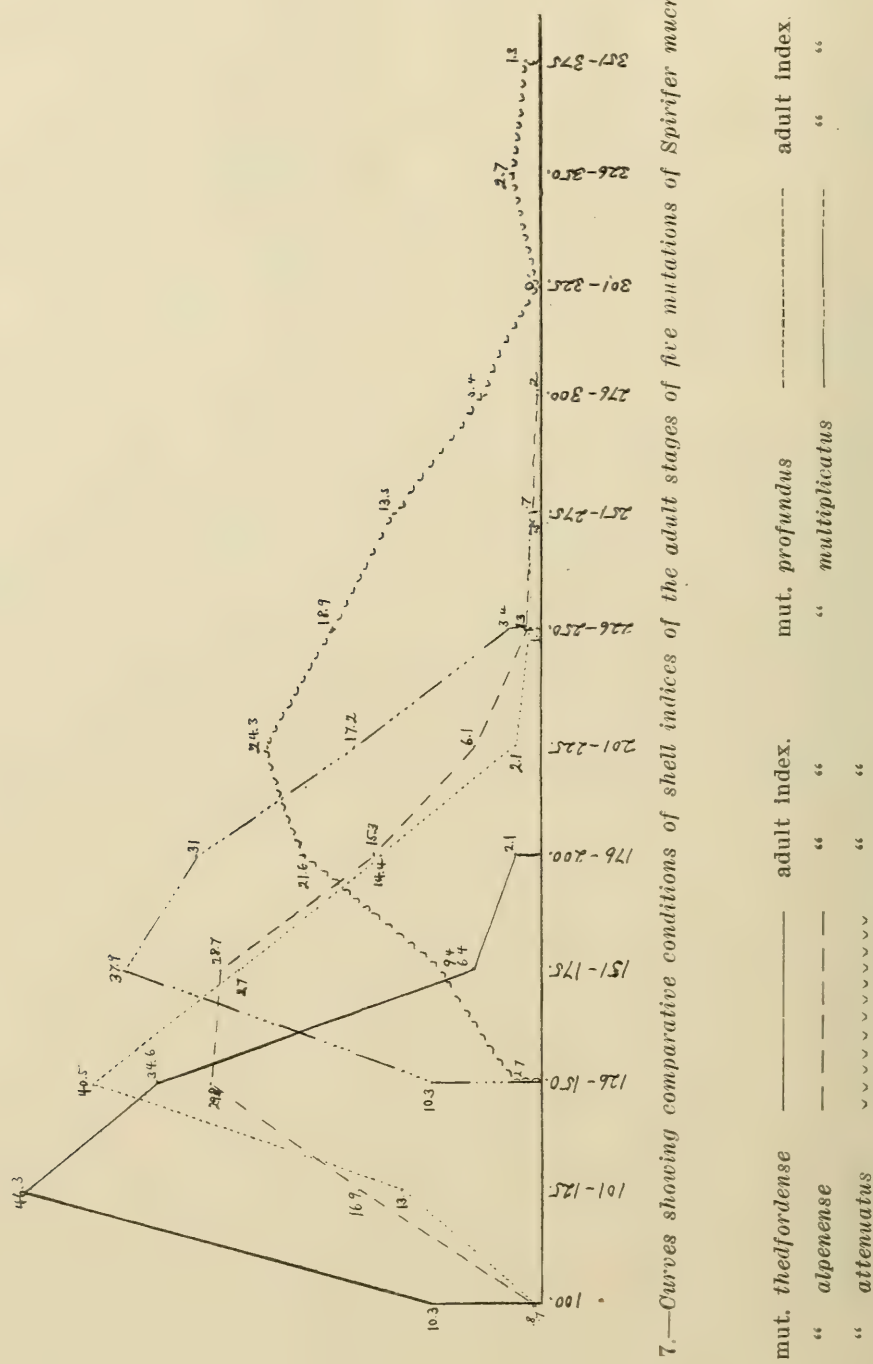


FIG. 7.—Curves showing comparative conditions of shell indices of the adult stages of five mutations of *Spirifer mucronatus*

mut. theifordense	adult index.	mut. profundus	adult index.
" alpenense	—	" multiplicatus	—
" attenuatus	~		~

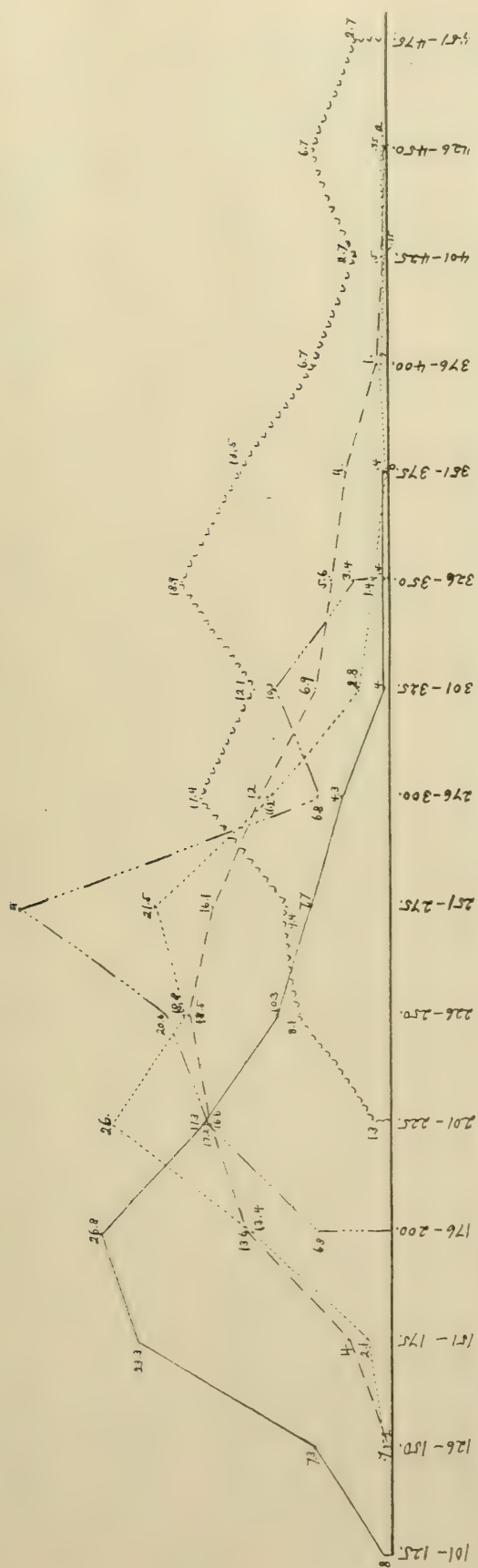


FIG. 8.—Curves showing comparative conditions of shell indices in neanic stages of five mutations of *Spirifer mucronatus*

mut. theldfordense	—————	neanic index.	— · — · —
“ alpenense	-----	“	-----
“ attenuatus	“
		mut. profundus	-----
		“ multiplicatus	-----

TABLES OF MEASUREMENTS AND INDICES

Spirifer mucronatus mut. *thedfordense*

Number	Adult Stage				Neanic Stage			
	Width	Height	Index (reverse)	Index	Width	Height	Index (reverse)	Index
1.....	31mm.	29mm.	.935	1.07	31mm.	23mm.	.741	1.34
2.....	32	29.5	.921	1.08	32	20.5	.640	1.56
3.....	32	27	.843	1.18	32	17	.531	1.88
4.....	38.5	27	.701	1.42	38.5	20.5	.532	1.87
5.....	30	30	1.000	1.00	30	24	.800	1.25
6.....	29	27.5	.948	1.05	29	19.5	.672	1.48
7.....	31	26.5	.854	1.16	31	19	.612	1.63
8.....	34	28	.823	1.21	34	23.5	.691	1.44
9.....	32	32.5	1.015	.98	32	18	.562	1.77
10.....	27	23	.851	1.17	27	17	.629	1.58
11.....	34	24	.705	1.41	34	19	.558	1.78
12.....	35	30.5	.871	1.14	35	19	.542	1.84
13.....	35	28	.800	1.25	35	17.5	.500	2.00
14.....	38	21.5	.565	1.76	38	16.5	.434	2.30
15.....	34	27	.794	1.25	34	22	.647	1.54
16.....
17.....	30	26	.866	1.15	30	20	.666	1.50
18.....	38	27.5	.723	1.38	38	18	.473	2.11
19.....	32	28	.875	1.14	32	20	.625	1.60
20.....	29	23	.793	1.26	29	19.5	.672	1.48
21.....	33	29.5	.893	1.11	33	18.5	.560	1.78
22.....	29	24	.827	1.20	29	17.5	.603	1.65
23.....	35	25	.714	1.40	35	18	.514	1.94
24.....	36	31	.861	1.16	36	21	.583	1.71
25.....	28	24.5	.875	1.14	28	17	.607	1.64
26.....	35	26	.742	1.34	35	22	.628	1.59
27.....	32	23.5	.734	1.36	32	17	.531	1.88
28.....	27	23	.851	1.17	27	19	.703	1.42
29.....	29	27	.931	1.07	29	21	.724	1.38
30.....	40.5	28	.691	1.44	40.5	20.5	.506	1.92
31.....	32.5	30	.923	1.08	32.5	17.5	.538	1.85
32.....	28	19	.678	1.47	28	15	.535	1.86
33.....	31.5	28.5	.904	1.10	31.5	18	.571	1.75
34.....	38	30	.789	1.26	38	23	.605	1.65
35.....	27	20	.740	1.35	27	14	.518	1.92
36.....	35	23	.657	1.52	35	18	.514	1.94
37.....
38.....	31	20	.645	1.55	31	14	.451	2.21
39.....	37.5	26	.693	1.44	37.5	20	.533	1.87
40.....	40	32	.800	1.25	40	23	.575	1.73
41.....	31	25	.806	1.24	31	17	.548	1.82
42.....	32	29	.906	1.10	32	19	.593	1.68

Spirifer mucronatus mut. *thedfordense*—Continued

Number	Adult Stage				Neanic Stage			
	Width	Height	Index (reverse)	Index	Width	Height	Index (reverse)	Index
43.....	29mm.	26mm.	.896	1.11	29mm.	20.5mm.	.706	1.44
44.....	31	30	.967	1.03	31	21	.677	1.47
45.....	27.5	29	1.054	.94	27.5	20	.727	1.37
46.....	32	25	.781	1.28	32	18	.562	1.77
47.....	29	26	.896	1.11	29	17	.586	1.70
48.....	33	25	.757	1.32	33	17	.515	1.94
49.....	32	24	.750	1.33	32	19	.593	1.68
50.....	30	25	.833	1.20	30	18	.600	1.66
51.....	29.5	22	.745	1.34	29.5	14	.474	2.10
52.....	37	26	.702	1.42	37	18	.432	2.05
53.....	31	27	.870	1.14	31	20	.645	1.55
54.....	37	24.5	.662	1.51	37	15.5	.418	2.38
55.....	30	24	.800	1.25	30	19	.633	1.57
56.....	32	25	.781	1.28	32	15.5	.484	2.06
57.....	28	21	.750	1.33	28	16	.571	1.75
58.....	32	23.5	.734	1.36	32	18	.562	1.77
59.....	33	26	.787	1.26	33	19	.575	1.73
60.....	27	23	.851	1.17	27	15	.555	1.80
61.....	30	26.5	.883	1.13	30	17	.566	1.76
62.....	27	26	.962	1.03	27	16	.592	1.68
63.....	34	23	.676	1.47	34	18	.529	1.88
64.....	40	25	.625	1.60	40	19	.475	2.10
65.....	33	24	.727	1.37	33	17	.515	1.94
66.....	39	30	.769	1.30	39	20	.512	1.95
67.....	29	24.5	.844	1.18	29	18.5	.638	1.56
68.....	40	21.5	.537	1.86	40	17.5	.437	2.28
69.....
70.....	40	29	.725	1.37	40	24	.600	1.66
71.....	38	27	.710	1.40	38	20	.521	1.90
72.....	28	21	.750	1.33	28	17	.607	1.64
73.....	35	26	.742	1.34	35	17.5	.500	2.00
74.....	39	25	.641	1.56	39	18.5	.474	2.10
75.....	34	29.5	.867	1.15	34	21	.617	1.61
76.....	32	26	.812	1.23	32	20	.625	1.60
77.....	26	25.5	.980	1.01	26	15	.576	1.73
78.....	29.5	24	.813	1.22	29.5	13.5	.457	2.18
79.....	29	25	.862	1.16	29	17.5	.603	1.65
80.....	29	25.5	.879	1.13	26	15.5	.596	1.67
81.....	31	25	.806	1.24	31	17	.548	1.82
82.....	29	16	.551	1.81	29	12	.413	2.41
83.....	28	15	.535	1.86	28	11	.392	2.54
84.....	32.5	21	.646	1.54	32.5	17.5	.538	1.85
85.....	31	25	.806	1.24	31	19.5	.629	1.58
86.....
87.....	34	20	.588	1.70	34	15	.441	2.26

Spirifer mucronatus mut. *thedfordense*—Continued

Number	Adult Stage				Neanic Stage			
	Width	Height	Index (reverse)	Index	Width	Height	Index (reverse)	Index
88.....	33.5mm.	26.5mm.	.791	1.26	33.5mm.	20mm.	.597	1.67
89.....	28	21.5	.767	1.30	28	17	.607	1.64
90.....	30	30	1.000	1.00	30	19	.633	1.52
91.....	34	25	.735	1.36	34	18	.529	1.88
92.....	39	27	.692	1.44	39	19	.482	2.05
93.....	34	26	.764	1.30	34	19	.558	1.78
94.....	34	25	.735	1.36	34	19	.558	1.78
95.....	34	23	.676	1.47	34	14	.411	2.42
96.....	43	29	.674	1.48	43	19	.441	2.26
97.....	31	30	.967	1.03	31	18.5	.596	1.67
98.....	35	24	.685	1.45	35	17.5	.500	2.00
99.....	27	26.5	.981	1.01	27	19.5	.722	1.38
100.....	39.5	32.5	.822	1.21	32.5	19	.584	1.71

101-175 inclusive = *Spirifer mucronatus* mut. *alpenense*.

213.....	33.5	32	.952	1.04	33.5	20	.597	1.675
214.....	27	25.5	.944	1.05	27	14	.518	1.92
215.....	32	31	.968	1.03	32	19	.593	1.68
216.....	26	28	1.076	.928	26	18	.692	1.44
217.....	30.5	28	.918	1.08	30.5	14	.459	2.17
218.....	33.5	32.5	.970	1.03	33.5	20	.597	1.675
219.....	26	26.5	1.019	.981	26	14.5	.557	1.49
220.....	35	33	.942	1.06	35	22.5	.642	1.55
221.....	27	27	1.000	1.000	27	18.5	.685	1.45
222.....	31	29	.935	1.06	31	20	.645	1.55
223.....	26	25	.961	1.04	26	17.5	.673	1.48
224.....	28	26	.928	1.07	28	22.5	.803	1.24
225.....	29	26	.896	1.11	29	20	.689	1.45
226.....	32	31	.968	1.03	32	22	.689	1.45

227-445 inclusive = *Spirifer mucronatus* mut. *alpenense*.

446.....	39.5	26.5	.670	1.49	39.5	17.5	.443	2.25
447.....	33	22	.666	1.50	33	14.5	.439	2.27
448.....	35	31	.885	1.12	35	17	.485	2.05
449.....	36	25.5	.708	1.41	36	20	.555	1.80
450.....	36	22.5	.625	1.60	36	16.5	.458	2.18
451.....
452.....	33	23.5	.712	1.40	33	16	.484	2.06
453.....	37	28.5	.770	1.29	37	18.5	.500	2.00
454.....	30	24	.800	1.25	30	17.5	.583	1.71
455.....	34	27	.794	1.25	34	22	.647	1.54
456.....	36	27.5	.763	1.30	36	20	.556	1.80
457.....	32	22.5	.703	1.42	32	14.5	.453	2.20
458.....	35	27	.771	1.29	35	19	.542	1.84
459.....	31	25	.806	1.24	31	18.5	.596	1.67
460.....	45	30	.666	1.50	45	21	.466	2.14

Spirifer mucronatus mut. *thedfordense*—Continued

Number	Adult Stage				Neanic Stage			
	Width	Height	Index (reverse)	Index	Width	Height	Index (reverse)	Index
461.....	36mm.	28mm.	.777	1.28	36mm.	21mm.	.583	1.71
462.....	32	29	.906	1.10	32	19.5	.609	1.64
463.....	33	28	.848	1.17	33	18.5	.560	1.78
464.....	35	26	.742	1.34	35	17	.486	2.05
465.....	30	22.5	.750	1.33	30	16.5	.550	1.81
466.....	33	23.5	.712	1.40	33	18	.545	1.83
467.....	36	23.5	.652	1.53	36	16	.444	2.25
468.....	30	24	.800	1.25	30	16	.533	1.875
469-605 inclusive = <i>Spirifer mucronatus</i> mut. <i>alpenense</i> .								
606.....	32	32	1.000	1.00	32	18	.562	1.77
607.....	31	31	1.000	1.00	31	17	.516	1.82
608.....	23	25	1.086	.92	23	11	.478	2.09
609.....	28.5	25	.877	1.14	28.5	15	.526	1.90
610.....
611.....	35	28	.800	1.25	35	13	.371	2.69
614.....	33	26	.757	1.26	33	15	.454	2.20
615.....	36	31	.861	1.16	36	20.5	.569	1.75
616.....
617.....	36	30	.833	1.20	36	14	.388	2.57
618.....	31.5	23.5	.746	1.34	31.5	17.5	.555	1.80
619.....
620.....	38	31.5	.828	1.20	38	18	.473	2.11
621.....
622.....	27	29	1.074	.931	27	16.5	.611	1.63
623.....	23.5	20.5	.711	1.14	23.5	12	.510	1.95
624.....	32	25	.781	1.28	32	16	.500	2.00
625.....	31	28	.903	1.10	31	18.5	.596	1.67
626.....
627.....	34	31.5	.926	1.07	34	15.5	.450	2.19
628.....	31	26	.838	1.19	31	12	.387	2.58
629.....
630.....	30	30.5	1.016	.983	30	18.5	.616	1.62
631.....	28	20	.714	1.40	28	11.5	.410	2.43
632.....	32	29.5	.921	1.08	32	18	.562	1.77
633.....	30	20	.666	1.50	30	13	.433	2.30
634.....	27	17	.629	1.58	27	11.5	.426	2.34
635.....	30	18	.600	1.66	30	10	.333	3.00
636.....	27.5	24	.872	1.14	27.5	13.5	.490	2.03
637.....	37.5	26	.693	1.44	37.5	17	.453	2.20
638.....	25.5	21	.823	1.21	25.5	10	.392	2.55
639.....	37	27.5	.743	1.34	37	17	.459	2.17
640.....	27	28	1.037	.964	27	16	.592	1.68
641.....	36	32	.888	1.125	36	18.5	.513	1.94
642.....	27	26	.962	1.03	27	10	.370	2.70
643.....	27	28.5	1.055	.947	27	16	.592	1.68

Spirifer mucronatus mut. *thedfordense*—Continued

Number	Adult Stage				Neanic Stage			
	Width	Height	Index (reverse)	Index	Width	Height	Index (reverse)	Index
644.....	31mm.	28mm.	.903	1.10	31mm.	15.5mm.	.500	2.00
645.....	27	23.5	.870	1.14	27	10.5	.388	2.57
646.....	27	26	.962	1.03	27	13	.481	2.07
647.....
648.....	29	17	.586	1.70	29	10	.344	2.90
651.....	32	35	1.093	.914	32	15	.468	2.13
652.....	29.5	26.5	.898	1.11	29.5	14.5	.491	2.03
653.....	31	34	1.096	.911	31	16.5	.532	1.87
654.....	38	31	.815	1.22	38	13	.342	2.92
655.....	31	25	.806	1.24	31	12.5	.403	2.48
658.....	25	26	1.040	.961	25	11	.440	2.27
659.....	30	31.5	1.050	.952	30	16	.503	1.875
660.....	24	20	.833	1.20	24	9	.379	2.66
661.....	27	27.5	1.018	.981	27	12	.444	2.25
662.....	37	19	.514	1.94	37	11	.297	3.36
663.....	31	27	.870	1.14	31	12	.387	2.58
664.....
665.....	30.5	20.5	.672	1.48	30.5	13.5	.442	2.25
666.....
667.....	30	29	.966	1.03	30	15.5	.516	1.93
668.....	24.5	27.5	1.122	.89	24.5	14.5	.604	1.68
669.....	27.5	27	.981	1.01	27.5	16	.581	1.71
670.....	31.5	27.5	.973	1.14	31.5	16.5	.523	1.96
671.....	30	21.5	.716	1.39	30	15.5	.516	1.93
672.....	31	27.5	.887	1.12	31	14.5	.467	2.13
673.....	40.5	27	.666	1.50	40.5	16	.395	2.53
674.....	31	24.5	.790	1.26	31	17	.548	1.82
675.....	39	24	.610	1.62	39	16.5	.423	2.36
676.....	35.5	30	.845	1.18	35.5	17.5	.494	2.02
677.....	43.5	27	.620	1.61	43.5	17.5	.402	2.48
678.....	32	26.5	.736	1.20	32	11	.343	2.90
679.....	31	23.5	.754	1.31	31	13	.419	2.38
680.....	39	28.5	.730	1.36	39	16.5	.428	2.36
681.....	37	25.5	.689	1.45	37	14	.378	2.64
682.....	40	28.5	.712	1.40	40	13.5	.437	2.96
683.....	34.5	25	.724	1.38	34.5	14	.405	2.46
684.....	34.5	27.5	.797	1.25	34.5	15.5	.449	2.22
685.....	37	29	.783	1.27	37	16.5	.445	2.24
686.....	37	25.5	.689	1.45	37	14	.378	2.64
687.....	32	32	1.000	1.00	32	18.5	.578	1.72
688.....	38	26.5	.697	1.43	38	13.5	.355	2.81
689.....	31	28.5	.919	1.08	31	17.5	.532	1.77
690.....	34	23.5	.691	1.44	34	14	.411	2.42

Spirifer mucronatus mut. *thedfordense*—Continued

Number	Adult Stage				Neanic Stage			
	Width	Height	Index (reverse)	Index	Width	Height	Index (reverse)	Index
691.....	36mm.	27mm.	.777	1.28	36mm.	15.5mm.	.430	2.32
692.....	29	26	.895	1.11	29	14.5	.500	2.00
693.....	33.5	25.5	.761	1.31	33.5	12.5	.373	2.68
694.....	28	27	.964	1.03	28	14	.500	2.00
695.....	35	29.5	.842	1.18	35	11	.314	3.17
696.....	31	22	.709	1.40	31	11.5	.370	2.69
697.....	37	22.5	.608	1.64	37	12.5	.337	2.96
698.....
699.....	39	26.5	.679	1.47	39	13	.333	3.00
700.....	30	30.5	1.016	.983	30	15	.500	2.00
701.....	30	23	.766	1.30	30	13.5	.450	2.22
702.....	42	34	.809	1.23	42	15	.357	2.80
703.....
704.....	36	29	.805	1.24	36	13.5	.375	2.66
705.....	31	31.5	1.016	.984	31	14.5	.403	2.13
706.....	31	29	.935	1.06	31	13.5	.435	2.29
707.....
708.....	35	23.5	.671	1.48	35	15	.428	2.33
709.....	34.5	28	.811	1.23	34.5	18	.521	1.97
710.....	31.5	26.5	.841	1.18	31.5	15.5	.492	2.03
711.....	30	24	.800	1.25	30	12.5	.416	2.40
712.....	36	36.5	1.013	.986	36	18	.500	2.00
713.....	36	29.5	.819	1.22	36	16	.444	2.25
714.....	33.5	29.5	.880	1.13	33.5	15	.447	2.23
715.....	29	26.5	.913	1.09	29	15.5	.536	1.87
716.....	33	29	.878	1.13	33	14	.424	2.35
717.....	36	30	.833	1.20	36	13	.361	2.76
718.....	40	27.5	.687	1.46	40	15.5	.387	2.58
719.....	41	29	.707	1.41	41	11.5	.280	3.56
720.....	38	29	.763	1.31	38	14	.368	2.71
721.....	41	29.3	.714	1.38	41	16	.390	2.56
722.....
723.....	29	25	.862	1.16	29	13	.448	2.23

Spirifer mucronatus mut. *alpenense*

101.....	38	22	.578	1.72	38	14	.367	2.71
102.....	34.5	20.5	.578	1.72	34.5	12.5	.362	2.76
103.....	35.5	19.5	.549	1.82	35.5	13	.366	2.73
104.....	34	21.5	.573	1.75	34	12	.352	2.83
105.....	32	20.5	.640	1.56	32	14	.437	2.28
106.....	29	17	.586	1.70	29	12.5	.431	2.32
107.....	38	19.5	.513	1.94	38	12.5	.328	3.04
108.....	27	16	.592	1.81	27	11	.403	2.45
109.....	32	23	.718	1.39	32	15	.468	2.13

Spirifer mucronatus mut. *alpenense*—Continued

Number	Adult Stage				Neanic Stage			
	Width	Height	Index (reverse)	Index	Width	Height	Index (reverse)	Index
110.....	30mm.	22mm.	.733	1.36	30mm.	15.5mm.	.516	1.93
111.....	41	20.5	.500	2.00	41	12	.292	3.41
112.....	26	11.5	.442	2.26	26	7.5	.288	3.46
113.....	32	20.5	.640	1.56	32	15	.468	2.13
114.....	25	17	.680	1.47	25	11.5	.460	2.17
115.....	29	18	.620	1.61	29	10	.344	2.90
116.....	31	19	.612	1.63	31	12	.387	2.58
117.....	39	21.5	.551	1.81	39	15	.384	2.60
118.....
119.....	38	18.5	.486	2.05	38	11	.289	3.45
120.....	34	22	.647	1.54	34	11	.323	3.09
121.....
122.....	32	22	.687	1.45	32	13	.406	2.46
123.....	40	24	.600	1.66	40	13	.325	3.07
124.....	38	19	.500*	2.00	38	13	.342	2.92
125.....	37	22	.594	1.68	37	12	.324	3.08
126.....	39.5	20	.506	1.97	39.5	11	.278	3.59
127.....	30	25	.833	1.20	30	11	.366	2.72
128.....	31	23	.741	1.34	31	12	.387	2.58
129.....	34	21	.617	1.65	34	12	.352	2.83
130.....	35	23	.657	1.52	35	11	.314	3.18
131.....	26	18	.692	1.44	26	10	.384	2.60
132.....	28	21.5	.767	1.30	28	11.5	.410	2.43
133.....	29	23	.793	1.26	29	11	.379	2.63
134.....	28	22	.785	1.27	28	11	.392	2.54
135.....	28	13	.464	2.15	28	6.5	.232	4.30
136.....	26	23	.884	1.13	26	13	.500	2.00
137.....	30	21	.700	1.42	30	12	.400	2.50
138.....	31	21	.677	1.47	31	12	.387	2.58
139.....	34	19.5	.573	1.74	34	10.5	.309	3.23
140.....	26	25	.961	1.04	26	14.5	.557	1.79
141.....	38	23	.605	1.65	38	11.5	.302	3.30
142.....	30	23	.766	1.30	30	12.5	.416	2.40
143.....	29	20	.689	1.45	29	11.5	.396	2.52
144.....	32	25	.781	1.28	32	14	.437	2.28
145.....	27	22	.814	1.22	27	11.5	.425	2.34
146.....	33	21	.636	1.57	33	12	.363	2.75
147.....	31	16.5	.532	1.87	31	12	.387	2.58
148.....	28	22.5	.803	1.24	28	12.5	.446	2.24
149.....	32	26	.812	1.23	32	14.5	.453	2.09
150.....	30	20	.666	1.50	30	14	.466	2.14
151.....	25	13.5	.540	1.85	25	9	.360	2.77
152.....	24	20	.833	1.20	24	18.5	.770	1.29
153.....	29	21	.724	1.38	29	13	.462	2.23
154.....	29	12	.413	2.11	29	9.5	.324	3.05

Spirifer mucronatus mut. *alpenense*—Continued

Number	Adult Stage				Neanic Stage			
	Width	Height	Index (reverse)	Index	Width	Height	Index (reverse)	Index
155.....	30mm.	22mm.	.733	1.36	30mm.	14.5mm.	.483	2.06
156.....	34	13	.382	2.61	34	9	.235	3.77
157.....	29	15	.517	1.93	29	11	.378	2.63
158.....	26	14.5	.557	1.79	26	10.5	.511	2.47
159.....	32	16.5	.512	1.93	32	12	.375	2.66
160.....	34	18	.529	1.88	34	12	.352	2.83
161.....	37.5	23	.613	1.62	37.5	13	.346	2.88
162.....	34	18	.529	1.88	34	10.5	.388	3.23
163.....	26	15	.576	1.73	26	8.5	.326	3.05
164.....	29.5	17	.576	1.73	29.5	10.5	.355	2.80
165.....	31	19.5	.629	1.58	31	12.5	.403	2.48
166.....	32	22	.687	1.45	32	13	.406	2.46
167.....	28	26	.928	1.07	28	13.5	.482	2.07
168.....	26	18.5	.711	1.40	26	10.5	.403	2.48
169.....	32	27	.845	1.18	32	16	.500	2.00
170.....	26	23.5	.903	1.10	26	17	.653	1.52
171.....	15	9	.600	1.66	15	7	.466	2.14
172.....	29	17	.586	1.70	29	11	.379	2.63
173.....	30	18	.600	1.66	30	11	.366	2.72
174.....	31	20	.645	1.55	31	15.5	.500	2.00
175.....	36	18.5	.513	1.94	36	12.5	.346	2.08
176.....	29	18	.620	1.61	29	11.5	.396	2.52
177.....	37.5	22	.586	1.70	37.5	11.5	.306	3.26
178.....	23	24	1.043	.96	23	14.5	.630	1.58
179.....	22	20	.909	1.10	22	11.5	.522	1.91
180.....	39	23	.589	1.69	39	16	.410	2.43
181.....	39.5	16	.405	2.46	39.5	11.5	.291	3.43
182.....	29	22	.758	1.31	29	16	.551	1.81
183.....	32	19.5	.609	1.64	32	13	.406	2.46
184.....	38	15.5	.407	2.45	38	11	.289	3.45
185.....	30	13	.433	2.30	30	9.5	.316	3.15
186.....	31	18.5	.596	1.67	31	14	.451	2.21
187.....
188.....
189.....
190.....	36	20.5	.569	1.75	36	13	.361	2.76
204.....	28	19	.678	1.47	28	13	.474	2.15
205.....	36	18.5	.513	1.94	28	11.5	.410	2.43
206.....
207.....	32	21	.656	1.52	32	14	.437	2.28
211.....	28	15	.535	1.86	28	12	.428	2.33
212.....	28	22	.785	1.22	28	9	.321	3.11
227.....	36	19.5	.541	1.84	36	15	.416	2.40

Spirifer mucronatus mut. *alpenense*—Continued

Number	Adult Stage				Neanic Stage			
	Width	Height	Index (reverse)	Index	Width	Height	Index (reverse)	Index
230.....	30mm.	16mm.	.533	1.87	30mm.	13mm.	.433	2.30
231.....	30	28.5	.950	1.05	30	15.5	.516	1.93
234.....	41	20.5	.500	2.00	41	16	.390	2.56
235.....	31	20	.645	1.55	31	14.5	.467	2.13
236.....	31	20	.645	1.55	31	14	.451	2.21
243.....	38	19.5	.513	1.94	38	12.5	.328	3.04
244.....	35	17	.473	2.05	35	9.5	.271	3.69
247.....	39	21	.538	1.85	39	10.5	.294	3.71
248.....	32	24	.750	1.33	32	15.5	.484	2.06
249.....
250.....	27	21	.777	1.23	27	15	.555	1.80
251.....
252.....	34	20	.588	1.70	34	12	.343	2.83
253.....	28	21	.750	1.33	28	12.5	.446	2.24
254.....	32	28	.875	1.14	32	12	.375	2.66
255.....	27.5	22.5	.818	1.22	27.5	15.5	.563	1.77
256.....	26	19.5	.750	1.33	26	14.5	.557	1.79
257.....	26	17	.653	1.52	26	9	.346	2.88
258.....	38	17.5	.480	2.17	38	11	.289	3.45
261.....	37	23	.621	1.60	37	14	.378	2.64
265.....	33	19.5	.590	1.69	33	13.5	.409	2.44
266.....
267.....	29	24	.827	1.20	29	16	.551	1.81
270.....	24	16.5	.687	1.45	24	10.5	.437	2.28
271.....	25	14	.560	1.78	25	8.5	.340	2.94
274.....	30	18.5	.616	1.62	30	14	.466	2.14
275.....	33	21.5	.651	1.53	33	16.5	.500	2.00
276.....	39	20.5	.525	1.90	39	12.5	.320	3.12
280.....	31	22	.709	1.40	31	18.5	.596	1.67
281.....	36	20	.555	1.80	36	11	.305	3.27
282.....	42	19	.452	2.21	42	12	.285	3.50
283.....	27	23	.851	1.17	27	14.5	.536	1.86
284.....
285.....	30	18	.600	1.66	30	11.5	.383	2.60
286.....	30	21	.700	1.42	30	15.5	.516	1.93
287.....	36	20.5	.625	1.75	36	13.5	.375	2.66
288.....	41	19	.463	2.15	41	10.5	.256	3.50
289.....
290.....	32.5	19.5	.600	1.66	32.5	11.5	.353	2.82

Spirifer mucronatus mut. *alpenense*—Continued

Number	Adult Stage				Neanic Stage			
	Width	Height	Index (reverse)	Index	Width	Height	Index (reverse)	Index
291.....	41mm.	20mm.	.487	2.05	41mm.	12mm.	.292	3.41
292.....
293.....	32	15.5	.484	2.06	32	10.5	.328	3.04
294.....
295.....	30	16.5	.550	1.81	30	11.5	.383	2.60
296.....	31	17.5	.564	1.77	31	14	.451	2.21
297.....
298.....	31	15.5	.500	2.00	31	9	.290	3.44
299.....
300.....	35	23	.657	1.52	35	14	.400	2.50
301.....
302.....	30	15.5	.516	1.93	30	8.5	.283	3.52
303.....	27	14	.518	1.92	27	7.5	.277	3.60
304.....	35	20	.571	1.75	35	12	.342	2.91
305.....
306.....	30	17.5	.583	1.77	30	11	.366	2.72
307.....	32	17	.531	1.88	32	12.5	.390	2.56
308.....	39	20.5	.525	1.90	39	12.5	.320	3.12
309.....	35	22.5	.643	1.55
310.....	25	17.5	.700	1.42	25	9	.360	2.77
311.....	34	23	.676	1.45	34	12.5	.367	2.72
312.....	26	15.5	.596	1.67	26	9	.346	2.88
313.....	33	22	.666	1.50	33	12.5	.378	2.62
314.....
315.....	36	16	.444	2.25	36	11.5	.319	3.13
316.....
317.....	26	15	.576	1.73	26	11	.423	2.36
318.....	37	18	.432	2.05	37	9	.243	4.11
319.....
320.....	38	18	.473	2.11	38	10.5	.276	3.62
321.....
322.....	26	16	.615	1.62	26	12	.461	2.16
323.....	37	19	.513	1.94	37	13	.348	2.84
324.....	32	27	.843	1.18	32	15	.468	2.13
325.....	26	12	.461	2.16	26	7.5	.280	3.46
326.....
327.....	31	18.5	.696	1.67	31	14	.451	2.21
328.....	27.5	19	.690	1.44	27.5	10.5	.381	2.61
329.....
330.....	38	19.5	.513	1.94	38	12.5	.328	3.04
331.....	30	20	.666	1.50	30	12.5	.416	2.40
332.....
333.....	25.5	14.5	.568	1.75	25.5	8	.313	3.18
334.....
335.....	26	17.5	.672	1.48	26	11	.423	2.36

Spirifer mucronatus mut. *alpenense*—Continued

Number	Adult Stage				Neanic Stage			
	Width	Height	Index (reverse)	Index	Width	Height	Index (reverse)	Index
338.....	29mm.	19.5mm.	.672	1.48	29mm.	11mm.	.379	2.63
339.....	29	21.5	.741	1.34	29	13.5	.462	2.14
340.....	29	20	.689	1.45	29	13	.448	2.21
341.....	27	16	.592	1.68	27	8.5	.314	3.64
342.....	35	23	.657	1.52	35	11.5	.325	3.04
343.....	32	17	.531	1.88	32	10.5	.324	3.04
344.....	29.5	24	.813	1.22	29.5	15.5	.525	1.90
345.....	27	24	.888	1.12	27	14	.518	1.92
348.....	29	18	.620	1.61	29	11	.379	2.63
349.....
350.....	28	18	.642	1.55	28	10	.357	2.80
351.....	33	16	.484	2.06	33	11	.333	3.00
352.....
353.....	27	20.5	.759	1.31	27	14	.518	1.92
354.....
355.....	34	19	.558	1.78	34	9.5	.279	3.57
356.....
357.....	34	22.5	.661	1.51	34	14	.411	2.42
361.....	34	19	.558	1.78	34	16	.470	2.12
364.....	33	19.5	.590	1.69	33	13	.393	2.53
365.....	29	17	.586	1.70	29	9	.310	3.22
366.....
367.....	39.5	18.5	.465	2.13	39.5	11	.278	3.59
373.....	26	23	.884	1.13	26	14.5	.557	1.79
374.....	32	21.5	.661	1.48	32	15.5	.484	2.06
375.....
376.....	25	15	.600	1.66	25	7	.280	3.57
377.....	30	12.5	.416	2.40	30	8	.266	3.75
378.....	31	20	.645	1.55	31	14	.451	2.21
379.....	30	15.5	.516	1.93	30	11.5	.383	2.60
380.....	27	16	.592	1.68	27	12.5	.462	2.16
381.....	21	20.5	.976	1.02	21	11	.523	1.90
382.....
383.....	35	21	.600	1.66	35	14.5	.414	2.41
384.....	27	17	.629	1.58	27	11	.407	2.45
385.....	29	16.5	.568	1.75	29	11.5	.396	2.52
386.....	31	18.5	.596	1.67	31	11	.354	2.81
387.....	25	16	.640	1.56	25	10.5	.420	2.38
388.....	35	20.5	.581	1.70	35	12.5	.357	2.80
389.....	36	19	.527	1.89	36	13	.361	2.76
390.....	36	13.5	.374	2.66	36	10	.277	3.60
391.....	29	19	.653	1.52	29	11.5	.396	2.52

Spirifer mucronatus mut. *alpenense*—Continued

Number	Adult Stage				Neanic Stage			
	Width	Height	Index (reverse)	Index	Width	Height	Index (reverse)	Index
392.....	35mm.	19mm.	.542	1.94	35mm.	12.5mm.	.357	2.80
393.....	38	17.5	.486	2.17	38	13.5	.355	2.81
394.....	31	20.5	.661	1.51	31	15.5	.500	2.00
395.....	23	15	.656	1.53	23	9.5	.413	2.41
396.....	38	17	.447	2.23	38	12	.315	3.16
397.....	35	16.5	.471	2.12	35	10.5	.300	3.33
398.....	24	15.5	.645	1.54	24	11	.458	2.18
399.....	27	19	.703	1.42	27	12	.444	2.25
400.....	29.5	19	.644	1.55	29.5	10	.338	2.95
401.....	30	21	.700	1.42	30	13	.433	2.30
402.....	33	16.5	.500	2.00	33	11	.333	3.00
403.....	36	17.5	.486	2.05	36	10.5	.291	3.42
404.....	26	16	.615	1.62	26	10.5	.403	2.47
405.....	35	18.5	.528	1.89	35	14.5	.414	2.41
406.....	39	21	.538	1.85	39	15	.384	2.60
407.....	27	14	.518	1.92	27	10	.370	2.70
408.....	22	12.5	.568	1.76	22	9	.409	2.44
409.....	33	19.5	.590	1.69	33	12.5	.375	2.64
410.....	20.5	16.5	.804	1.24	20.5	10.5	.512	1.95
411.....	30	21	.700	1.42	30	14	.466	2.14
412.....	27	15	.555	1.80	27	9.5	.351	2.84
413.....	26	20	.769	1.30	26	12.5	.480	2.08
414.....	26	18.5	.711	1.40	26	12.5	.480	2.08
415.....	29	20	.689	1.46	29	11.5	.396	2.52
416.....	27	20.5	.759	1.31	27	13	.481	2.07
417.....	28	17.5	.625	1.60	28	10.5	.375	2.64
418.....	27.5	20.5	.745	1.31	27.5	14	.509	1.96
419.....	27.5	20.5	.745	1.31	27.5	15	.545	1.83
420.....	28	21	.750	1.33	28	14	.500	2.00
421.....	27	20	.740	1.35	27	11.5	.425	2.34
422.....	26.5	20.5	.773	1.29	26.5	14	.528	1.89
423.....	28	23.5	.839	1.19	28	17	.607	1.64
424.....	26	23	.884	1.13	26	16.5	.634	1.57
425.....	27	14.5	.537	1.86	27	10	.370	2.70
426.....	26.5	19	.716	1.39	26.5	12	.452	2.20
427.....	26	21	.807	1.23	26	13	.500	2.00
428.....	30	18.5	.616	1.62	30	11.5	.383	2.60
429.....	27.5	18	.654	1.52	27.5	12.5	.454	2.20
430.....	28	20	.714	1.40	28	12.5	.446	2.24
431.....	26	18.5	.714	1.40	26	13.5	.519	1.92
432.....	26.5	21.5	.811	1.20	26.5	14.5	.547	1.82
433.....	25	18	.720	1.38	25	12.5	.500	2.00
434.....	27	23.5	.870	1.14	27	17	.629	1.58
435.....	30	22.5	.750	1.33	30	14.5	.483	2.06
436.....	33	21.5	.651	1.52	33	11.5	.348	2.86

Spirifer mucronatus mut. *alpenense*—Continued

Number	Adult Stage				Neanic Stage			
	Width	Height	Index (reverse)	Index	Width	Height	Index (reverse)	Index
437.....	29mm.	19.5mm.	.672	1.48	29mm.	11.5mm.	.396	2.52
438.....	27	19.5	.709	1.38	27	9.5	.351	2.84
439.....	29	22	.758	1.31	29	17	.586	1.70
440.....	30	19	.633	1.57	30	14	.466	2.14
441.....	32	20	.625	1.60	32	14	.437	2.28
442.....	29	18	.620	1.61	29	10.5	.362	2.76
443.....	29	13.5	.465	2.14	29	10	.344	2.90
444.....	22	11	.500	2.00	22	9	.409	2.44
445.....	26.5	19	.716	1.39	26.5	11.5	.433	2.30
446-468 inclusive = <i>Spirifer mucronatus</i> mut. <i>thedfordense</i> .								
469.....	32	20	.625	1.60	32	12.5	.390	2.56
470.....	32	21	.656	1.52	32	13.5	.421	2.37
471.....	28	20	.714	1.40	28	13	.464	2.15
472.....	28	26	.928	1.07	28	16	.571	1.75
473.....	35	23	.657	1.52	35	16	.457	2.18
474.....	32	19	.593	1.76	32	12.5	.390	2.56
475.....	32	20	.625	1.60	32	13	.406	2.46
476.....	29.5	20	.677	1.47	29.5	12	.407	2.45
477.....	25	17	.680	1.47	25	12	.480	2.08
478.....	29.5	24	.814	1.22	29.5	15	.508	1.96
479.....	28.5	22	.771	1.29	28.5	14.5	.508	1.96
480.....	31	21	.677	1.47	31	13	.419	2.38
481.....	30	21	.700	1.42	30	13	.433	2.30
482.....	38	18.5	.486	2.05	38	13	.342	2.92
483.....	31.5	23	.730	1.36	31.5	12.5	.396	2.52
484.....	29.5	22.5	.763	1.31	29.5	14	.474	2.10
485.....	32	23	.718	1.39	32	10.5	.327	3.04
486.....
487.....	36	21	.583	1.71	36	12	.333	3.00
488.....
489.....	31	20.5	.661	1.51	31	14.5	.475	2.13
490.....	26	22	.846	1.18	26	11.55	.442	2.26
491.....	31	21.5	.693	1.44	31	13.5	.435	2.29
492.....	31	17.5	.564	1.77	31	12.5	.403	2.48
493.....	25	22	.880	1.13	25	14	.560	1.78
494.....	30	17.5	.583	1.71	30	13.5	.450	2.22
495.....
496.....	28	21.5	.767	1.25	28	11	.392	2.54
497.....	26	21	.807	1.23	26	15	.577	1.73
498.....	24	21.5	.895	1.11	24	15	.625	1.60
499.....	27	22	.814	1.22	27	11	.407	2.44
500.....	29	23	.793	1.26	29	12	.413	2.41
501.....	30	21	.700	1.42	30	13	.433	2.30
502.....	35	23	.657	1.52	35	13.5	.385	2.59

Spirifer mucronatus mut. *alpenense*—Continued

Number	Adult Stage				Neanic Stage			
	Width	Height	Index (reverse)	Index	Width	Height	Index (reverse)	Index
503.....	25mm.	19mm.	.760	1.31	25mm.	12mm.	.480	2.08
504.....	33	24.5	.742	1.34	33	15.5	.499	2.12
505.....	33.5	21	.626	1.59	33.5	10	.298	3.35
506.....	27	22.5	.833	1.20	27	14	.518	1.92
507.....	36	21	.583	1.71	36	12.5	.347	2.88
508.....	30	23	.766	1.30	30	10.5	.350	2.85
509.....	28	19.5	.696	1.43	28	10.5	.375	2.66
510.....	28	19.5	.696	1.43	28	13.5	.482	2.07
511.....	28	24	.856	1.16	28	13	.464	2.15
512.....	25	21	.840	1.19	25	14	.560	1.78
513.....	36	26.5	.736	1.35	36	16.5	.458	2.18
514.....	28	21	.750	1.33	28	13.5	.482	2.07
515.....	32	23.5	.734	1.36	32	9	.281	3.55
516.....	30	21	.700	1.42	30	9	.300	3.33
517.....	40	19	.475	2.10	40	11	.275	3.63
518.....	30	17.5	.583	1.71	30	10	.333	3.00
519.....
520.....	30	22	.733	1.36	30	12.5	.416	2.40
521.....	26	26	1.000	1.00	26	13.5	.519	1.92
522.....	26	15.5	.596	1.67	26	8.5	.326	3.05
523.....	31	15.5	.500	2.00	31	8	.258	3.87
524.....	29	22	.758	1.31	29	12.5	.431	2.32
525.....
526.....	35	21.5	.614	1.62	35	10	.285	3.50
527.....	25	22	.880	1.13	25	9.5	.380	2.63
528.....	27	21	.777	1.28	27	12.5	.462	2.16
529.....	31	19	.612	1.63	31	10.5	.338	2.95
530.....	28	21	.750	1.33	28	13	.464	2.15
531.....	30	19	.633	1.57	30	10.5	.350	2.85
532.....	35	22	.628	1.59	35	11	.314	3.18
533.....	27	18.5	.611	1.45	27	9	.333	3.00
534.....	29	19	.655	1.52	29	8	.275	3.62
535.....	30	20.5	.683	1.46	30	10	.333	3.00
536.....	24	21.5	.895	1.11	24	14	.583	1.71
537.....	26	22.5	.865	1.15	26	13	.500	2.00
538.....	24	19.5	.812	1.23	24	10.5	.437	2.28
539.....	25	21	.840	1.19	25	13	.520	1.92
540.....	26	20	.769	1.30	26	14	.576	1.85
541.....	26	18	.692	1.44	26	10	.384	2.60
545.....	24	19	.791	1.26	24	12	.500	2.00
546.....	24	19	.791	1.26	24	7	.291	3.42
547.....	37.5	24	.640	1.56	37.5	12	.320	3.12
548.....	23	19	.826	1.21	23	9.5	.413	2.42
549.....	24	17.5	.729	1.37	24	10	.416	2.40

Spirifer mucronatus mut. *alpenense*—Continued

Number	Adult Stage			Index	Neanic Stage			
	Width	Height	Index (reverse)		Width	Height	Index (reverse)	Index
550.....	28mm.	21.5mm.	.767	1.30	28mm.	13mm.	.464	2.15
551.....	24	19	.791	1.26	24	12	.500	2.00
552.....	28	14	.500	2.00	28	11	.392	2.54
553.....	27	22.5	.833	1.20	27	10	.370	2.70
554.....	29	18	.620	1.61	29	12	.413	2.41
555.....	24	22	.916	1.09	24	13	.541	1.84
556.....	34	21.5	.632	1.58	34	13.5	.397	2.51
557.....	27	19	.703	1.42	27	12	.444	2.25
558.....	28	19	.678	1.47	28	13	.464	2.15
559.....	31	21.5	.687	1.44	31	11	.354	2.81
560.....	25	22.5	.900	1.11	25	11	.440	2.27
561.....	25	12.5	.500	2.00	25	11	.440	2.27
562.....	27	17.5	.648	1.54	27	11	.407	2.45
563.....	24	23	.958	1.04	24	15	.625	1.60
564.....	29	20.5	.706	1.41	29	14.5	.500	2.00
565.....	31	21	.677	1.47	31	14	.451	2.21
566.....	27	23	.851	1.17	27	13.5	.500	2.00
567.....	30	24	.800	1.25	30	15	.500	2.00
568.....	30	20	.666	1.50	30	13	.433	2.30
569.....	33	27	.818	1.22	33	14	.423	2.35
570.....	27	23	.851	1.17	27	16	.592	1.68
571.....	25	24	.960	1.04	25	10	.400	2.50
572.....	31	27	.870	1.14	31	14	.451	2.21
573.....	28	20	.714	1.40	28	14	.500	2.00
574.....	28	20	.714	1.40	28	14.5	.517	1.93
575.....	29	24	.827	1.20	29	14	.483	2.07
576.....	25	20	.800	1.25	25	13.5	.540	1.85
577.....	30	22	.733	1.36	30	13	.433	2.30
578.....	26	22	.846	1.17	26	14	.538	1.85
579.....	26	14	.538	1.85	26	11	.423	2.36
580.....	28	18	.642	1.55	28	12	.428	2.33
581.....	30	18	.600	1.66	30	11.5	.388	2.60
582.....	28	22.5	.803	1.24	28	11.5	.410	2.43
583.....	31	16.5	.532	1.87	31	8	.254	3.87
584.....	25	21	.840	1.19	25	12	.480	2.08
585.....	36	22	.611	1.63	36	13	.361	2.76
586.....	28	22	.785	1.27	28	14.5	.517	1.93
587.....	25	24	.960	1.04	25	14.5	.604	1.72
588.....	27	19.5	.722	1.38	27	12	.444	2.25
589.....	27	17	.629	1.58	27	9	.333	3.00
590.....	19.5	13	.666	1.50	19.5	7.5	.384	2.53
591.....	30.5	20.5	.672	1.48	30.5	12.5	.409	2.44
592.....	32	17.5	.546	1.82	32	9.5	.296	3.36
593.....	28	23	.821	1.21	28	15	.534	1.86
594.....	27	15.5	.574	1.74	27	10.5	.388	2.57

Spirifer mucronatus mut. *alpenense*—Continued

Number	Adult Stage				Neanic Stage			
	Width	Height	Index (reverse)	Index	Width	Height	Index (reverse)	Index
595.....	25mm.	25mm.	1.000	1.00	25mm.	15mm.	.600	1.66
596.....	35	12.5	.357	2.80	35	9.5	.271	4.10
597.....	33	22	.666	1.50	33	13	.393	2.53
598.....
599.....	29.5	20	.677	1.47	29.5	11	.372	2.68
600.....	24	15.5	.645	1.56	24	10	.416	2.40
601.....	28	20	.714	1.40	28	13	.464	2.15
602.....	28	18.5	.660	1.51	28	11	.392	2.54
603.....	29.5	20	.677	1.47	29.5	11.5	.389	2.96
604.....	28.5	19.5	.684	1.46	28.5	12	.421	2.37
605.....	30	13.5	.450	2.22	30	9	.300	3.33

Spirifer mucronatus mut. *profundus*

801....	23	15	.652	1.53	23	11.5	.500	2.00
802....	24	13.5	.562	1.77	24	9.5	.395	2.52
805....	22	15.5	.704	1.41	22	11.5	.522	1.91
806....	27	18	.666	1.50	27	13	.481	2.07
807....	25	17	.680	1.47	25	9	.360	2.77
808....	30	16	.533	1.87	30	11	.366	2.72
809....	28	15	.535	1.86	28	10	.357	2.80
810....	23	16	.695	1.43	23	9	.391	2.55
811....	27	15	.555	1.80	27	11	.407	2.45
812....	28	16	.571	1.75	28	11	.392	2.54
813....	23	15	.652	1.53	23	11	.478	2.09
814....	22	19	.863	1.16	22	15	.681	1.46
815....	21	14	.666	1.50	21	11.5	.547	1.82
816....
817....	22	15	.681	1.46	22	9	.409	2.44
818....	34	18	.529	1.88	34	10	.294	3.40
819....	22.5	11	.493	2.04	22.5	8	.355	2.81
820....	22	19	.863	1.15	22	12	.545	1.83
821....	25	20	.800	1.25	25	14	.560	1.78
822....	27	16	.518	1.68	27	10	.370	2.70
823....	19	13	.684	1.46	19	9.5	.500	2.00
824....	22	13	.590	1.69	22	8.5	.386	2.58
825....	23	17.5	.760	1.31	23	11	.478	2.09
826....	23	19.5	.847	1.17	23	11	.478	2.09
827....	19.5	14	.717	1.39	19.5	12.5	.641	1.56
828....	19	19	1.000	1.00	19	10	.526	1.90
829....	26	18	.692	1.44	26	10	.384	2.60
830....	20	17.5	.875	1.14	20	9	.450	2.22
831....	21	15.5	.738	1.35	21	10.5	.500	2.00
832....	23	16	.695	1.43	23	12	.521	1.91
833....	27	15.5	.574	1.74	27	10	.370	2.70

Spirifer mucronatus mut. *profundus*—Continued

Number	Adult Stage				Neanic Stage			
	Width	Height	Index (reverse)	Index	Width	Height	Index (reverse)	Index
834....	20mm.	13mm.	.650	1.53	20mm.	8mm.	.400	2.50
835....	28	15	.535	1.86	28	10	.357	2.80
836....	20	13	.650	1.53	20	9	.450	2.22
837....	24	16	.666	1.50	24	9	.375	2.66
838....	29	16	.551	1.81	29	10	.344	2.90
839....	19.5	13.5	.692	1.42	19.5	8.5	.435	2.29
840....	20	14	.700	1.42	20	9.5	.475	2.10
841....	18	12.5	.694	1.44	18	8	.466	2.25
842....	25	14	.560	1.78	25	9	.360	2.77
843....	19	17	.894	1.11	19	11	.578	1.72
844....	23	15.5	.673	1.48	23	9	.347	2.55
845....	24	15	.625	1.60	24	9	.375	2.66
846....	27	13.5	.500	2.00	27	9.5	.351	2.80
847....
848....	17.5	15	.857	1.16	17.5	9	.514	1.94
849....	29	14	.482	2.07	29	10	.344	2.90
850....	30	15.5	.516	1.93	30	9.5	.316	3.15
851....	27	16	.592	1.68	27	10.5	.388	2.57
852....
853....	18	12.5	.694	1.44	18	7	.388	2.57
854....	19	10	.526	1.90	19	6.5	.342	2.90
855....	25	15	.600	1.66	25	9	.360	2.77
856....	24	15	.625	1.60	24	9	.375	2.66
857....	27	14	.518	1.92	27	9.5	.351	2.08
858....	25.5	18	.705	1.41	25.5	10.5	.411	2.42
859....	19.5	13.5	.692	1.44	19.5	8	.410	2.68
860....	24	15	.625	1.60	24	10	.416	2.40
861....	23	16	.695	1.43	23	10.5	.456	2.19
862....	22	11	.500	2.00	22	6.5	.295	3.38
863....	23	15.5	.673	1.48	23	9	.391	2.55
864....	22.5	13.5	.600	1.66	22.5	9.5	.422	2.36
865....	20	17	.850	1.17	20	9	.450	2.22
866....	23	13	.565	1.77	23	9	.391	2.55
867....	22	16.5	.750	1.33	22	11	.500	2.00
868....	20	12	.600	1.66	20	8	.400	2.50
869....
870....	23.5	11	.468	2.13	23.5	8	.340	2.93
871....
872....	24	14	.583	1.71	24	9	.375	2.66
873....	24	16.5	.687	1.45	24	10	.416	2.40
874....	28	17	.607	1.64	28	10	.357	2.80
875....	22	15.5	.704	1.41	22	9	.409	2.44
876....
877....	23.5	15.5	.659	1.51	23.5	9	.382	2.61
878....	23	12	.521	1.91	23	8	.347	2.87

Spirifer mucronatus mut. *profundus*—Continued

Number	Adult Stage				Neanic Stage			
	Width	Height	Index (reverse)	Index	Width	Height	Index (reverse)	Index
879....
880....	20mm.	14mm.	.700	1.42	20mm.	8mm.	.400	2.50
881....	24	18	.750	1.33	24	8.5	.354	2.82
882....	26	20.5	.788	1.26	26	10.5	.403	2.47
883....	21	16.5	.785	1.27	21	10	.476	2.10
884....	18.5	14.5	.783	1.27	18.5	10.5	.567	1.76
885....	21	15	.714	1.40	21	9	.428	2.33
889....	28	17	.607	1.64	28	11	.392	2.54
890....
891....	22	12	.545	1.83	22	8.5	.386	2.58
892....	24	15.5	.645	1.62	24	9	.375	2.66
893....
894....	25	16.5	.660	1.51	25	9	.360	2.77
895....	24	16	.666	1.50	24	9	.375	2.66
896....	20	13.5	.675	1.48	20	8.5	.425	2.35
897....	21	14	.666	1.50	21	9	.428	2.33
898....	20	11	.650	1.81	20	7	.350	2.85
899....	25.5	16	.627	1.59	25.5	10	.392	2.55
900....	24.5	12	.489	2.04	24.5	9	.367	2.72
901....	24	16	.666	1.50	24	10.5	.437	2.24
902....
903....	21.5	15	.697	1.43	21.5	7.5	.348	2.86
904....
905....	18	16	.858	1.12	18	9.5	.527	1.89
906....	16	13.5	.843	1.18	16	7	.437	2.28
907....	16	13.5	.843	1.18	16	8	.500	2.00
908....	28	16	.571	1.75	28	10.5	.375	2.66
909....
910....	17	11.5	.676	1.47	17	8	.470	2.12
911....	22.5	17	.755	1.32	22.5	10	.444	2.25
912....	20	13.5	.675	1.48	20	8	.400	2.50
913....	17	11	.647	1.55	17	8	.470	2.12
914....	18	12.5	.694	1.44	18	8	.466	2.25
915....	19.5	14	.717	1.39	19.5	7.5	.384	2.60
916....
917....	23	14	.608	1.64	23	8.5	.369	2.70
918....	19	13.5	.710	1.40	19	8.5	.447	2.02
919....
920....	20.5	17.5	.814	1.17	20.5	8	.390	2.56
921....	19	12	.631	1.56	19	7.5	.384	2.60
922....
923....	17.5	14	.800	1.25	17.5	8	.457	2.18
924....	23	12	.521	1.91	23	9	.347	2.55
925....	18	13.5	.750	1.33	18	8	.444	2.25

Spirifer mucronatus mut. *profundus*—Continued

Number	Adult Stage				Neanic Stage			
	Width	Height	Index (reverse)	Index	Width	Height	Index (reverse)	Index
926....	21mm.	13mm.	.619	1.61	21mm.	8mm.	.380	2.62
927....	25	13	.520	1.92	25	8	.320	3.12
928....	19	15	.673	1.26	19	9	.421	2.11
929....	27	20	.740	1.35	27	10	.370	2.70
930....	17.5	15	.857	1.16	17.5	9	.514	1.94
931....	17	14	.823	1.21	17	7	.411	2.42
932....	19	15.5	.815	1.22	19	8.5	.447	2.23
933....	23	12.5	.543	1.84	23	8.5	.369	2.70
934....	21	15	.714	1.40	21	8	.352	2.12
935....	30	20	.666	1.50	30	10.5	.350	2.85
936....	24	10.5	.479	2.28	24	8	.333	3.00
937....	35	14.5	.414	2.51	35	8	.228	4.37
938....	18	13	.722	1.38	18	7.5	.416	2.40
939....	20	14.5	.725	1.37	20	8.5	.425	2.35
940....	18	11.5	.638	1.56	18	7	.388	2.57
941....	24	14	.583	1.71	24	7	.291	3.42
942....	24	14.5	.604	1.64	24	9	.375	2.66
943....	22	13	.590	1.69	22	7	.318	3.14
944....	18	12	.666	1.50	18	6.5	.361	2.76
945....	15	12	.800	1.25	15	7.5	.500	2.00
946....	21	14	.666	1.50	21	8	.380	2.12
947....	27	19.5	.722	1.37	27	11.5	.425	2.34
948....	21.5	14	.651	1.53	21.5	8	.372	2.68
949....	19	12	.631	1.58	19	8	.421	2.37
950....	20	12	.600	1.66	20	7.5	.375	2.66
951....	16	10	.625	1.60	16	7.5	.468	2.13
952....	22	17	.772	1.29	22	10.5	.477	2.09
953....	18	12	.666	1.50	18	8	.444	2.25
954....	19	14.5	.763	1.31	19	9.5	.500	2.00
955....	18.5	15	.818	1.23	18.5	8.5	.459	2.17
956....	21	15	.714	1.40	21	9	.428	2.33
957....	22.5	16.5	.777	1.36	22.5	12	.533	1.87
958....	21	16	.761	1.31	21	9	.428	2.33
959....	19	15.5	.815	1.22	19	9	.421	2.11
960....
961....	18	15	.833	1.20	18	10	.555	1.80
962....	25	16	.640	1.56	25	12	.480	2.08
963....
964....	22	12	.545	1.83	22	8.5	.386	2.58
965....	21	14	.666	1.50	21	9	.428	2.33
966....	21.5	13	.604	1.65	21.5	9	.418	2.38
967....	18	13	.722	1.38	18	9.5	.527	1.89
968....	18.5	10.5	.567	1.76	18.5	8	.432	2.31
969....	21	14	.666	1.50	21	10.5	.500	2.00
973....	19	12	.631	1.58	19	7.5	.394	2.53

Spirifer mucronatus mut. *profundus*—Continued

Number	Adult Stage				Neanic Stage			
	Width	Height	Index (reverse)	Index	Width	Height	Index (reverse)	Index
974....	25mm.	16mm.	.640	1.56	25mm.	10mm.	.400	2.50
975....
976....	21.5	15	.697	1.43	21.5	10	.465	2.15
977....
978....	22	11.5	.522	1.91	22	7.5	.380	2.93
979....	18	13	.722	1.38	18	8	.444	2.25
980....	15	9	.600	1.66	15	8	.533	1.87
981....
982....	18	13	.722	1.38	18	7.5	.416	2.40
983....	18.5	12	.643	1.54	18.5	8	.432	2.31
984....	20	12.5	.625	1.60	20	9.5	.475	2.10
985....	17.5	12	.685	1.45	17.5	7.5	.428	2.33
988....	29	12	.413	2.41	29	7.5	.258	3.86
989....	18	11.5	.638	1.56	18	7.5	.416	2.40
990....	21.5	15.5	.720	1.38	21.5	10.5	.488	2.64
991....	17	11	.647	1.54	17	7.5	.441	2.26
995....	19	14	.736	1.35	19	8.5	.447	2.23
996....
997....	25	16	.640	1.56	25	10.5	.420	2.38
998....	19	13	.684	1.46	19	9	.421	2.11
999....	22	16	.727	1.37	22	11	.500	2.00
1000....
1001....	21.5	16	.744	1.34	21.5	9	.418	2.38
1002....	23.5	18	.765	1.30	23.5	11.5	.489	2.04
1003....	29	14	.482	2.71	29	9	.310	3.22
1004....	20	12.5	.625	1.60	20	9	.450	2.22
1005....	22.5	14	.622	1.60	22.5	10	.444	2.25
1006....	35	18	.514	1.94	35	12	.342	2.91
1007....	28	18.5	.660	1.51	28	11.5	.410	2.43
1008....	23	18	.782	1.28	23	10	.434	2.30
1009....	20	19	.950	1.05	20	12	.600	1.66
1010....	22	13.5	.613	1.62	22	10	.454	2.20
1011....	25.5	18	.713	1.41	25.5	11	.431	2.31
1012....	20	14	.700	1.42	20	9.5	.475	2.10
1013....	25.5	16	.627	1.59	25.5	9	.352	2.83
1014....	19	12	.631	1.38	19	7	.368	2.71
1015....	19	17	.894	1.11	19	11	.578	1.72
1016....	20	14.5	.725	1.37	20	9	.450	2.20
1017....	27	20	.740	1.35	27	13	.481	2.07
1018....
1019....	22	19	.863	1.15	22	10	.454	2.20
1020....
1021....	22	18	.818	1.22	22	10.5	.477	2.09
1022....	20	12	.600	1.66	20	9	.450	2.22

Spirifer mucronatus mut. *profundus*—Continued

Number	Adult Stage				Neanic Stage			
	Width	Height	Index (reverse)	Index	Width	Height	Index (reverse)	Index
1023....	22mm.	18mm.	.818	1.22	22mm.	12mm.	.545	1.83
1024....	26	18	.692	1.44	26	11	.426	2.36
1025....	22	21	.954	1.04	22	10	.454	2.20
1026....	24	15	.625	1.60	24	9	.375	2.66
1027....	28.5	16	.561	1.78	28.5	9.5	.333	3.00
1028....	22	16.5	.750	1.33	22	10	.454	2.20
1029....	25	18	.720	1.38	25	11	.440	2.27
1030....	18	15	.833	1.20	18	10.5	.583	1.71
1035....	22	16	.727	1.37	22	10	.454	2.20
1036....	23	13	.565	1.76	23	8	.347	2.87
1037....	18	12	.666	1.50	18	7	.389	2.59
1038....	28	16.5	.589	1.69	28	10.5	.375	2.66
1039....	18	10	.555	1.80	18	7.5	.416	2.40
1040....	20	15	.750	1.33	20	8.5	.425	1.35
1041....	19.5	12.5	.641	1.56	19.5	9.5	.487	2.05
1042....	24.5	19	.775	1.28	24.5	12	.489	2.04
1043....	20	13.5	.675	1.48	20	10	.500	2.00
1044....	21	16	.761	1.31	21	10.5	.500	2.00
1045....	28	16	.571	1.75	28	11	.392	2.54
1046....	25	15	.600	1.66	25	12	.480	2.09
1047....	28	14	.500	2.00	28	9	.321	3.11
1048....	23	16.5	.717	1.39	23	10.5	.456	2.19
1049....	21	13	.619	1.61	21	9	.428	2.66
1050....	18	14.5	.805	1.24	18	9	.500	2.00
1051....	19	13	.684	1.46	19	8	.421	2.37
1052....	18	12	.666	1.50	18	8.5	.461	2.11
1053....	18	13	.611	1.38	18	10	.555	1.80
1054....	20.5	12.5	.609	1.62	20.5	9	.439	2.27
1055....
1056....	22	18	.555	1.80	22	10.5	.477	2.07
1057....	23	16.5	.717	1.39	23	12	.521	1.91
1058....
1059....	35	14	.400	2.50	35	11	.314	3.18
1060....	27	16	.592	1.68	27	10.5	.388	2.57
1061....	25	16	.640	1.56	25	10.5	.420	2.38
1062....	20.5	14	.682	1.46	20.5	9	.439	2.27
1063....	31	18	.580	1.72	31	10.5	.338	2.95
1064....	24	16	.666	1.50	24	11	.458	2.17
1065....	24	15.5	.645	1.54	24	7	.291	3.42
1066....	29	15.5	.534	1.87	29	9	.310	3.22
1067....	26	13.5	.519	1.92	26	9	.346	2.88
1068....	25	21	.840	1.19	25	11	.440	2.27
1069....	23	12.5	.543	1.84	23	8	.347	2.87
1070....	28	14.5	.517	1.93	28	11	.392	2.54
1071....	26.5	18	.679	1.47	26.5	11	.415	2.40

Spirifer mucronatus mut. *profundus*—Continued

Number	Adult Stage				Neanic Stage			
	Width	Height	Index (reverse)	Index	Width	Height	Index (reverse)	Index
1072....	29mm.	13.5mm.	.465	2.14	29mm.	7mm.	.241	4.14
1073....	20	13	.650	1.53	20	9	.450	2.22
1074....	22.5	12	.533	1.87	22.5	8.5	.377	2.05
1075....	26	12	.461	2.16	26	9	.346	2.88
1076....	28	20	.714	1.40	28	11.5	.410	2.60
1077....	26	14.5	.557	1.79	26	9.5	.365	2.73
1078....
1079....	24	13.5	.562	1.77	24	10	.416	2.40
1080....
1081....	28	15	.535	1.86	26	9.5	.365	2.73
1082....	26	17	.653	1.52	26	11	.423	2.36
1101....	24	18	.750	1.33	24	11	.458	2.18
1102....	20	13.5	.675	1.48	20	9	.450	2.22
1103....	21	12.5	.595	1.68	21	9	.428	2.33
1104....
1105....	22	17.5	.795	1.28	22	11	.500	2.00
1106....	27	16.5	.611	1.63	27	11	.407	2.54
1107....	21	15	.714	1.40	21	10	.476	2.10
1108....	22	15	.681	1.46	22	10	.454	2.20
1109....	32	20	.625	1.60	32	12	.375	2.66
1110....	26.5	18	.679	1.47	26.5	11	.415	3.77
1111....	21.5	14	.651	1.52	21.5	10	.465	2.15
1112....	23	15.5	.674	1.67	23	11	.478	2.09
1113....	24	17	.708	1.41	24	11	.468	2.18
1114....	22	17	.772	1.29	22	10	.454	2.20
1115....
1116....	23.5	16.5	.702	1.42	23.5	11.5	.489	2.04
1117....	25.5	19	.744	1.34	25.5	12	.470	2.12
1118....	20	16	.800	1.25	20	9	.450	2.22
1119....	26	14.5	.557	1.79	26	9	.346	2.88
1120....	27	17	.629	1.58	27	12	.444	2.25
1121....	21	15	.714	1.40	21	9	.428	2.66
1122....	21	19	.904	1.10	21	10	.476	2.10
1123....	22	17.5	.795	1.25	22	9.5	.431	2.31
1124....	17	15	.882	1.13	17	9	.529	1.88
1125....
1126....	21	15	.714	1.40	21	11	.523	1.90
1127....	21	13	.619	1.61	21	8	.380	2.62
1130....	20.5	15	.731	1.36	20.5	8	.381	2.56
1131....	34	13	.541	1.84	24	9	.375	2.66
1132....	17	17.5	1.029	.97	17	9.5	.556	1.78
1133....	28	17	.607	1.64	28	12.5	.446	2.24
1134....
1135....	24.5	13	.530	1.88	24.5	8	.326	3.06

Spirifer mucronatus mut. *profundus*—Continued

Number	Adult Stage				Neanic Stage			
	Width	Height	Index (reverse)	Index	Width	Height	Index (reverse)	Index
1136....	18.5mm.	14.5mm.	.789	1.27	18.5mm.	8mm.	.432	2.56
1137....	18.5	15	.810	1.23	18.5	9.5	.513	1.94
1138....
1139....	22	15	.681	1.46	22	10	.454	2.20
1140....	18	11.5	.638	1.56	18	9	.500	2.00
1141....	22	16	.727	1.37	22	12	.545	1.83
1142....	21.5	15	.697	1.43	21.5	9	.418	2.38
1143....	20	13	.650	1.53	20	10	.500	2.00
1144....	20	16.5	.825	1.21	20	11.5	.575	1.73
1145....	24	20	.833	1.20	24	11.5	.479	2.86
1146....	21	14	.666	1.50	21	9	.428	2.66

Spirifer mucronatus mut. *multiplicatus*

1201....	41	20.5	.500	2.00	41	14	.341	2.92
1202....	38	21	.552	1.80	38	12.5	.328	3.04
1203....	32.5	19.5	.600	1.66	32.5	12.5	.384	2.60
1204....
1205....	28	17	.607	1.64	28	13	.464	2.15
1206....	33	22.5	.681	1.46	33	18.5	.560	1.78
1207....	41	22	.536	1.86	41	17	.414	2.41
1208....	30	16	.533	1.87	30	11	.366	2.72
1209....	27.5	18	.654	1.52	27.5	14	.509	1.96
1210....
1211....	50	21.5	.460	2.32	50	16	.320	3.12
1212....	35	20	.571	1.75	35	13	.371	2.69
1213....	41.5	25	.602	1.66	41.5	18	.433	2.30
1214....	39	26	.666	1.50	39	16	.410	2.43
1215....	32	15	.468	2.13	32	10	.312	3.20
1216....	36	24.5	.680	1.46	36	17	.472	2.11
1217....	46	22.5	.489	2.04	46	18	.391	2.55
1218....	39	19	.487	2.05	32	15.5	.484	2.06
1219....	42	21.5	.511	1.95	42	16	.380	2.62
1220....	44	21.5	.488	2.04	44	15	.340	2.93
1221....	42	20	.476	2.10	42	12	.285	3.50
1222....	38.5	20	.519	1.92	38.5	15	.380	2.56
1223....	38	22	.578	1.72	38	14	.368	2.71
1224....	32	17	.531	1.88	32	12	.375	2.66
1225....
1226....	30	18	.600	1.66	30	13	.433	2.30
1227....	31	15.5	.500	2.00	31	12.5	.403	2.48
1228....
1229....	26	15	.576	1.86	26	10.5	.403	2.47
1230....	43	27	.627	1.59	43	16	.372	2.68
1231....	33	21	.636	1.57	33	15.5	.469	2.12
1232....	32	20.5	.640	1.56	32	15.5	.484	2.06
1233....	33	20.5	.621	1.60	33	13	.393	2.53

Spirifer mucronatus mut. *attenuatus*—Continued

Number	Adult Stage				Neanic Stage			
	Width	Height	Index (reverse)	Index	Width	Height	Index (reverse)	Index
1350....	33mm.	10mm.	.303	3.30	33mm.	7.5mm.	.227	4.40
1354....	36	15.5	.430	2.32	36	10	.272	3.60
1355....	24	14	.583	1.71	24	9	.375	2.66
1356....	35	17	.485	2.05	35	11	.314	3.18
1357....	33	15	.454	2.20	33	9.5	.257	3.47
1358....	31	17	.548	1.82	31	12.5	.403	2.48
1359....	44	16	.363	2.75	44	10.5	.238	4.19
1360....	36	14	.388	2.57	36	11	.305	3.27
1361....	36	13	.361	2.76	36	9	.250	4.00
1362....	31	13.5	.435	2.29	31	9	.290	3.44
1363....	32	11	.343	2.90	32	7.5	.234	4.26
1364....	31	17.5	.564	1.77	31	11	.354	2.81
1365....
1366....	25	12	.480	2.08	25	8.5	.340	2.94
1367....	32	13	.406	2.46	32	10	.312	3.20
1368....	30	13.5	.450	2.22	30	9.5	.316	3.15
1369....	32	14	.437	2.28	32	9	.281	3.55
1370....
1371....	35	13.5	.385	2.59	35	10	.285	3.50
1372....	34	14	.411	2.48	34	9	.264	3.77
1373....	42	15	.357	2.80	42	9.5	.226	4.42
1374....	34	17	.500	2.00	34	11.5	.338	2.95
1375....	28	12.5	.446	2.24	28	8.5	.303	3.29
1376....	31.5	16	.507	1.96	31.5	11.5	.365	2.73
1377....	35	15	.441	2.26	34	10	.291	3.40
1378....
1379....	29	13	.448	2.23	29	9.5	.327	3.05
1380....	26	12	.461	2.16	26	7	.269	3.71
1383....	25	13	.520	1.92	25	8.5	.340	2.94
1384....	34	14	.411	2.42	34	9.5	.279	3.57
1385....	23	13	.565	1.76	23	7.5	.326	3.06
1386....	35	15	.428	2.33	35	9	.257	3.88
1387....	24	11.5	.479	2.08	24	8	.333	3.00
1390....	26	12	.461	2.16	26	8.5	.326	3.05
1391....	39.5	15.5	.392	2.54	39.5	9	.227	4.38
1392....	29	12	.413	2.41	29	8	.275	3.62
1393....	27	12	.444	2.25	27	7.5	.277	3.60
1394....	25	9	.360	2.77	25	6.5	.260	3.84
1395....	28	11	.392	2.54	28	7.5	.267	3.73
1396....	29	13.5	.465	2.14	29	8.5	.293	3.41

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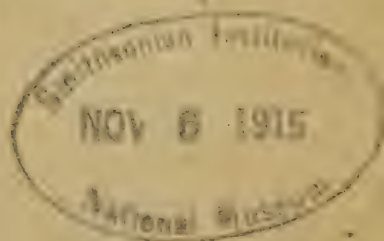
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PLEISTOCENE OF EUROPE, ASIA AND
NORTHERN AFRICA

BY

HENRY FAIRFIELD OSBORN



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REVIEW OF THE PLEISTOCENE OF EUROPE, ASIA AND NORTHERN AFRICA¹

BY HENRY FAIRFIELD OSBORN

(Presented by title before the Academy, 12 April, 1915)

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¹ Revision for German edition of the author's work, "The Age of Mammals;" German translator and editor, Dr. W. O. Dietrich, Kgl. Geologisch-palæontologisches Institut und Museum, Berlin.

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INTRODUCTION

We observe that the Upper Tertiary closes with a Pliocene northern world rich with life, a world replete with Asiatic and African influence. The Tertiary Period is followed by the Quaternary, or Age of Man, a time of transition and of vast extinctions in Europe and North America through natural causes, as well as of the geographic redistribution of life and establishment of the modern zoögeographic regions. Toward the close of the Quaternary Period man becomes the "destroying angel" and very nearly completes the havoc which Nature has begun.

CÆNOZOIC.

Quaternary Age of Man

Tertiary Age of Mammals

We thus enter a new Cænozoic faunal phase, the Seventh. When its transitions are complete the world wears an entirely new and somewhat impoverished aspect: the North has banished all the chief southerly forms and established the five modern zoölogical regions of the Old and New Worlds, namely: Palæarctic. Nearctic. Oriental. Ethiopian. Neotropical.

SEVENTH FAUNAL PHASE—QUATERNARY

IN THE NORTHERN HEMISPHERE THE GLACIAL EPOCH. VERY GRADUAL EXTINCTION OR EXPULSION OF SOUTHERN TYPES OF AFRICAN, SOUTH ASIATIC AND SOUTH AMERICAN ORIGIN FROM THE NORTHERN, OR HOLARCTIC REALM. FIRST APPEARANCE IN CENTRAL EUROPE AND NORTH AMERICA OF THE CIRCUMPOLAR TUNDRA FAUNA, IN EUROPE OF THE STEPPE FAUNA. IN NORTH AMERICA EXTINCTION OF THE REMAINING LARGE ENDEMIC QUADRUPEDS. THIRD AND FINAL MODERNIZATION OF EUROPE AND NORTH AMERICA BY THE HARDY FOREST, MEADOW AND MOUNTAIN RUMINANTS AND THE CARNIVORES.

The grand geologic divisions of the Quaternary in the New and Old Worlds are the same, namely, beginning with the Pleistocene and closing with the Holocene.

- QUATERNARY {
- II. HOLOCENE. OR RECENT EPOCH. Mammals of prehistoric and recent times. Domestication.
 - I. PLEISTOCENE. OR GLACIAL EPOCH.
 - 3. POSTGLACIAL. Mammals of tundra and steppe type gradually disappearing or retreating. Mammals of existing north temperate type multiplying.
 - 2. GLACIAL. Period of successive glacial advances and interglacial retreats. Mammals of extinct and existing species commingled.
 - 1. PREGLACIAL. Period of the lowering of temperature in the northern hemisphere and modification of plant and animal life.

MEANS OF ESTABLISHING THE TIME DIVISIONS OF THE QUATERNARY

The fluctuations of climate and of the plant and animal life of the Pleistocene are so numerous, so widespread, and so profound that it seems best to introduce the subject by a review of the great time divisions

together with some discussion as to the period when we should consider that the Quaternary proper begins. The fullness and precision of European faunistic investigation is in very strong contrast to the preliminary results of American work, and in no other period may we anticipate more weighty inductions from correlation between the history of the Old and New Worlds. It is absolutely clear that a final and positive time scale and subdivision of the early Age of Man are not far distant and that the vast labors of European and American geologists, botanists, zoölogists, palæontologists and anthropologists will finally be rewarded with a harmonious theory of all the phenomena of the Quaternary Period, the determination of the chronology of the various races and an approximate estimate of the duration of the entire Quaternary Period itself. The reader will observe that this correlation, derived from at least five distinct branches of natural science, is based on evidence of four kinds.

1. Geological: glacial deposits and erosions, which furnish the chief data for estimates of time.
2. Botanical: plant deposits, alternations of northern, arctic, steppe, temperate and southern floras, which furnish the chief data for estimates of temperature.
3. Palæozoölogical: evolution and extinction of mammal and bird life, which furnish the chief divisions of the Quaternary time scale and afford supplementary knowledge of conditions of moisture, temperature and forestation.
4. Anthropological: the successive stages of human culture and implements, the skeletal remains of man, which combined furnish the minor subdivisions and correlations of Quaternary time.

PLIOCENE AND PLEISTOCENE LIFE OF ASIA AND NORTH AFRICA

LIFE OF ASIA

The region of the rich Tertiary flood plains of India² was one of the main sources of the large mammals which wandered into northern Africa and southern Europe in Pleistocene times; in other words, the large mammals—the elephants, the rhinoceroses, the hippopotami—were all invading forms from Asia and Africa. The relations between these three geographic regions are, in fact, so close that they might be embraced in a single zoögeographic realm were it not that throughout the Pleistocene the forests and meadows of southern Europe also maintained a northern Eurasiatic fauna which is entirely absent from southern Asia.

² See p. 323, English edition of "The Age of Mammals."

TABLE I.—Classification of the Tertiary Flood-Plain Deposits of India. Pilgrim, 1913

Classification	Characteristic Fossils	Feet above base of Siwaliks	European Horizons
Upper Siwaliks . . .	Boulder conglomerate zone	14, 000–16, 000	Uppermost Pliocene
	Pinjar horizon . .	11, 500–14, 000	Middle to Upper Pliocene
	Tatrot horizon . . .	10, 000–11, 500	Lower Pliocene
	Bhandar beds	9, 500–10, 000	Uppermost Pontian or Lowest Pliocene
Middle Siwaliks . . .	Dhok Pathan horizon	8, 500–9, 500	Upper Pontian (stage of Pkermi). Upper Miocene
	Nagri horizon	5, 500	Lower Pontian. Upper Miocene
Base of Middle Siwaliks		4, 000

Lower Siwaliks ...	Upper Chinji horizon	<i>Hipparion</i> (scarce), <i>Sus</i> , <i>Hyootherium</i> , <i>Palaeoryx</i> , <i>Protragocerus</i> , <i>Giraffokeryx</i> , <i>Amphicyon paleindicus</i> , <i>Hyana</i> , <i>Sivapithecus</i> (probably most of the Lower Chinji species)	3,200-4,000	Uppermost Sarmatian. Middle Miocene
	Lower Chinji horizon	<i>Tetrabelodon macrognathus</i> and sp. var., <i>Hyootherium</i> cf. <i>siudense</i> , <i>Isotridon</i> , <i>Sus</i> , <i>Hemimeryx pusillus</i> , <i>Protragocerus</i> and small antelopes, <i>Giraffokeryx</i> , <i>Propalaeomeryx</i> , <i>Dorcacabueanthracotheroides</i> , <i>Amphicyon</i> aff. <i>giganteus</i> , <i>Haplogale</i> , <i>Dissopsalis</i> , <i>Dryopithecus</i>	1,700-3,200	Sarmatian (stage of Saint Gaudens)
	Lower Manchhar horizon	<i>Tetrabelodon angustidens</i> and <i>pandionis</i> , <i>Aceratherium gajense</i> var., <i>Brachyodus</i> , <i>Hyoboaops</i> , <i>Hemimeryx blanfordi</i> , <i>Telmatodon</i> , <i>Hyootherium siudense</i> , <i>Propalaeomeryx</i> cf. <i>exigua</i>	Base-1,700	Tortonian (stage of Simorre). Middle Miocene
Murree	Upper Murree or Kasauli	<i>Sabal major</i> and plant remains	Helvetian to Tortonian
	Lower Murree or Dagshai	Unfossiliferous	Max. thickness, 8,000	Burdigalian to Helvetian. Lower Miocene
Gaj	Kuldana	<i>Anthracootherium bugliense</i> , <i>Teloceras fatchjungense</i> , <i>Brachyodus africanus</i>
	Bugti beds	<i>Anthracootherium bugliense</i> , <i>Brachyodus giganteus</i> and <i>africanus</i> , <i>Hemimastodon crepusculi</i> , <i>Mastitherium</i> , <i>Teloceras blanfordi</i> , <i>Telmatodon bugtensis</i> , <i>Cadurcootherium indicum</i>	Max. thickness, 1,000	Lower Burdigalian or Upper Aquitanian. Upper Oligocene.

The precise researches of Pilgrim,³ published subsequent to the correlation proposed by the author in 1910 in the Pliocene chapter of the "Age of Mammals,"⁴ have resulted in a new classification and correlation of the Tertiary flood-plain deposits of India which are of the utmost importance and interest to students both of phylogeny and of geographic distribution and migration.

In geologic time the Indian series extends from the Bugti beds, which are of Aquitanian or Upper Oligocene age, to the uppermost Pliocene of the Upper Siwaliks. The correlation with the successive intermediate phases of European life appears to be quite close.

As regards the origin of the Proboscidea, the author discovers in the Upper Oligocene of India animals which he believes resemble the Lower Oligocene *Palæomastodon* as well as the *Mærittherium* of the Fayûm deposits of northern Egypt. These animals are referred to respectively as *Hemimastodon* and *Mærittherium*. This discovery would favor the hypothesis that the Proboscidea may have originated in southern Asia rather than in Africa. Pilgrim believes that the *Mastodon cautleyi* of the Upper Miocene of Perim Island gave rise to the *Stegodon* types of the uppermost Miocene of Pikermi age, namely, to *S. clifti* and *S. bombifrons*, from which originated the genus *Elephas* which first appears in the dominant type *Elephas planifrons* of Middle to Upper Pliocene times in strata 3,000 feet above those in which the earliest forms of *Stegodon* occur.

The species *E. planifrons* is especially important because it has recently been recognized by Schlesinger⁵ in the Pliocene "Belvederschotter" north of Dobermannsdorf near Vienna. The horizon is regarded as of Middle Pliocene or even earlier age. Pavlow⁶ has also recorded the occurrence of *E. planifrons* from beds in Bessarabia which are regarded as of Lower Pliocene age. In the Upper Pliocene of Europe occurs *Elephas meridionalis* which is regarded as a descendant of *E. planifrons*, while in the Upper Pliocene of India occurs the *Elephas hysudricus*, which Pohlig considers as a geographic variety of the European *E. meridionalis*. In the uppermost Pliocene of India also occurs the *Dicerorhinus platyrhinus*, which is believed to be closely related to the *D. etruscus* of the Upper Pliocene of the Val d'Arno of Italy.

Some authors mistakenly regard the "Altelephant" (*E. antiquus*) of

³ PILGRIM, GUY E.: "The Correlation of the Siwaliks with Mammal Horizons of Europe." Records, Geol. Surv. India, Vol. xliii, Part 4, pp. 264-326, Pl. 26. 1913.

⁴ See Life of Southern Asia, pp. 323-332, "Age of Mammals."

⁵ SCHLESINGER, PAUL: "Studien über die Stammesgeschichte der Proboscidiæ," Jahrb. d. k. Geol. Reichs., Vol. 62, pp. 87-182. Vienna, 1912.

⁶ PAVLOW, MARIE: "Les éléphants posttertiaires de diverses localités en Russie." Ann. géol. et minéralog. de la Russie, vol. xi, pp. 171-174. Moscou, 1910.

the European Pleistocene as related to *E. hysudricus* of India, but Pilgrim and Pohlig rightly compare *E. antiquus* with the Narbada elephant (*E. namadicus*), which first occurs in the Pleistocene of Asia. In fact, it is not known whether the phylum of *E. antiquus*, which is quite distinct from that of *E. planifrons*-*E. Meridionalis*, originated in Asia or in Africa.

To sum up, among the contributions of southern Asia to the Pliocene and Pleistocene fauna of Europe are the following:

Elephas planifrons, entering Europe in the Pliocene, related to the *Elephas meridionalis*, the southern elephant.

Elephas hysudricus.

Hippopotamus, *H. javadicus*, related to *H. major*.

Bison sivalensis, the short-skulled bison, related to *Bison priscus*.

The long-skulled *Leptobos*, related to the *L. etruscus* of the Val d'Arno and *Bos primigenius* of the First Interglacial Stage.

The Sumatran type of rhinoceros, *Dicerorhinus platyrhinus*, related to *D. etruscus* and *D. merckii*.

The hyænas, related to *H. crocuta*, the spotted hyæna, and *H. striata*, the striped hyæna.

The horse, *Equus sivalensis*, related to the Arab, or desert type of Europe.

Among the mammals which did not find their way from Asia into western Europe are the camels and the various giraffoids. The absence of the antelopine members of the Bovidæ is also a very characteristic feature of the Pleistocene of Europe as contrasted with their abundance in Asia and their presence in diminished form and numbers in the Upper Pliocene of Europe.

LIFE OF NORTH AFRICA

It would appear that in Lower Pleistocene times when there were broad land connections between Europe and Africa the latter continent contributed to Europe some of its indigenous mammals and others which had been derived originally from Asia. It is natural to suppose that the hyæna and hippopotamus, now so characteristic of Africa, entered Europe either from Asia or from the north African region. With these animals may have come the lion (*Felis leo*) and the "old elephant" (*E. antiquus*), which is a primitive offshoot of the same stock that gave rise to the African elephant (*Loxodon africanus*).

We observe that in Lower Pleistocene times north Africa is still distinctively a part of the Ethiopian Region, closely connected with central and southern Africa in its fauna. Throughout the Lower Quaternary the fauna of north Africa is also closely related to that of Asia. Moreover it has a number of species in common with the Quaternary fauna of

Europe, including those noted below which came into Europe from Africa. The contrary theory of the relative geographic isolation of Africa and Europe in Quaternary times originated with Pomel¹ as the result of his exhaustive review of the entire fauna of north Africa. He concludes that since the resemblances between the European and north African faunas are rare and often doubtful, the two continents were for long periods separated by the Mediterranean Sea and Straits of Gibraltar.

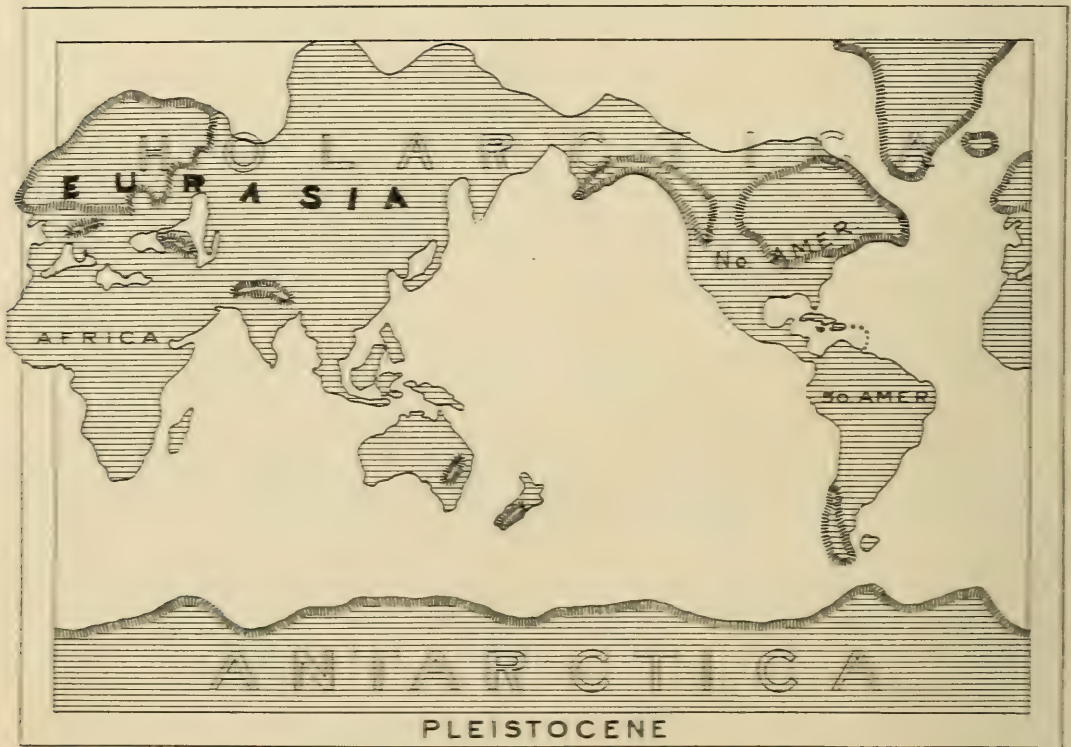


FIG. 1.—Pleistocene, or Ice Age

A period of maximum total elevation facilitating free migrations and invasions of life, culminating in the Glacial epoch, and followed by a prolonged depression. Portions of northern Europe and the coasts of North America greatly depressed. Then a period of re-elevation. Rearranged after W. D. Matthew, 1908.

Climate.—At the beginning of the Quaternary Period north Africa was characterized by abundant rainfall which led to the formation of great alluvial or flood-plain depositions. In the Barbary and Sahara regions the life was closely similar to the grand plateau life of equatorial Africa at the present time, including elephants, rhinoceroses, zebras, wild asses, giraffes, wild cattle, buffalo, antelopes, gazelles, gnus, elands, hippopotami, wart-hogs, lions and hyenas. The presence of these ani-

¹ POMEL, A.: "Les Éléphants Quaternaires." *Carte Géol. Algérie, Paléont. Monogr.* Algiers, 1895.

mals is consistent with the climatic theory of subtropical temperature and alternate dry and rainy seasons.

Various phenomena point to increasingly long periods of drought and progressive secular desiccation of this great region as the Pleistocene advanced, resulting in the partial extinction and partial migration of the great equatorial life into central and southern Africa.

Eurasiatic Invasion.—At the close of the Quaternary the bear (*Ursus*), as a characteristic forest-dweller, requiring a moist climate, became extinct, while the Eurasiatic deer, wild sheep, wild boar, smaller mammals of European type, survived and established for this region its present affinity with Europe and its Palæarctic fauna. We must account for this northerly, or Eurasiatic, fauna of north Africa as having entered the continent during the latter part of the Pleistocene Epoch and as surviving in the forested regions of present and prehistoric times so as to unite northern Africa closely with modern and prehistoric Europe. North Africa thus becomes a part of the Palæarctic Region.

Thus in no region of the world have more profound changes occurred during and since Pleistocene times than in Africa north of the Sahara Desert.

Sources of the Pleistocene African Life.—It is premature to attempt to ascertain the original sources of all the various members of this imposing assemblage of mammals. There remains always a great element of doubt which can be eliminated only by the discovery of the complete Cænozoic history of Asia and Africa. It would appear probable from our previous studies that the several continents contributed to the remote original ancestry of the African fauna somewhat as follows:

Africa or Asia, elephants and mastodons.

Northern Eurasia, deer and bear, wild sheep, wild boar.

Southern Eurasia, wild cattle and buffalo.

North America or northern Eurasia, rhinoceroses, various *Equidae*, camels.

The most comprehensive comparison of the fauna of Africa and Europe is that of Stromer,⁸ in which the entire fauna of Europe and north Africa, including the Reptilia and Mammalia, is compared from Lower Eocene to Pleistocene times. This author observes⁹ that during the middle period of the Tertiary the mammal fauna of southwestern Europe, western Asia, India to China, partook of the tropical or subtropical

⁸ STROMER, ERNST: "Über die Bedeutung der fossilen Wirbeltiere Afrikas für die Tiergeographie." Verhandl. d. Deutsch. Zoöl. Gesellschaft, pp. 204-218. 1906.

⁹ STROMER, ERNST: "Die einstige Verbreitung afrikanischer Säugetiere." Naturwissenschaftliche Wochenschrift, N. F., X Band; der ganzen Reihe, XXVI Band, No. 51, pp. 814-816. Dec. 17, 1911.

character of the African high plateau fauna, rich in antelopes, giraffes, zebra-like ancestors of the horse, elephants, rhinoceroses, hyænas and apes. Late in Diluvial times in Europe numerous representatives of what we now consider a tropical African fauna, including hippopotami, lions, hyænas and apes, were widely distributed.

Asiatic and European Affinities.—The total assemblage of the Pleistocene life of north Africa may be summarized as follows from Pomel:

Man (*Homo*, Late Pleistocene)
 Mastodon (Early Pleistocene only)
 Elephants (several species related both to *Loxodon* and to *Elephas*)
 Rhinoceroses (two species of the African, or *Diceros* type)
 Hipparions, zebras and asses
 Camels
 Giraffes (*Libytherium*, *Giraffa*)
 Wild cattle (*Bos*), three species
 Buffalo (*Bubalus*)
 Dwarf antelopes, gazelles, gnus, oryx, nagor, elands
 Hippopotami
 Wild boar (*Sus*)
 Wart hogs (*Phacochærus*)
 Lions (two cavern species)
 Hyænas (spotted and striped)
 Jackals (*Canis aureus*), India
 Macaques (of northern origin)
 Deer (of the *Cervus* type, one species)
 Bear (of the *Helarctos* group)
 Wild sheep and goats (*Ovis palæotragus*, *O. promaza*)

latter species only occurs in the recent deposits of the latest prehistoric period.

Similarly the two species of rhinoceros (*D. mauritanicus*, *D. subinermis*) resemble the modern African types, but there is nothing to indicate the presence either of the modern African "black" (*D. bicornis*) or "white" (*D. simus*) species.

Among the Pleistocene horses, in addition to the surviving hipparions and the species (*E. numidicus*) related to the Val D'Arno type of Europe, there is a third species (*E. mauritanicus*) which exhibits tooth characters of the recent zebra. Thus there is every reason to believe that

A noteworthy distinction between north Africa and Europe is the survival in north Africa of the mastodons throughout early Pleistocene times; also of several species of hipparions side by side on the plains of Numidia with the early north African horses¹⁰ or zebras. Both the mastodons and the hipparions are absent in the Pleistocene of Europe.

We may now review the life of north Africa itself in Pleistocene times. Six species of elephant occur, including the mastodons, the southern mammoth (*E. meridionalis*), and the "old elephant" (*L. antiquus*). The most characteristic and widespread elephant (*L. atlanticus*) belongs to the African subgenus *Loxodon* while differing from the recent African elephant (*L. africanus*) in several points. The

¹⁰ BOULE, M.: "Observations sur quelques Équidés Fossiles." Bull. Soc. Géol. France, Ser. 3, vol. xxvii, pp. 531-542. 1899.

in Pleistocene times ancestors of the zebras, which are now confined to equatorial Africa, extended to the extreme north of the continent. To the same period belongs a wild ass very similar to the Ethiopian ass (*E. asinus*), an animal which survived in this region until exterminated by the Greeks and Romans, and is now confined to the highlands of Abyssinia.

Among the Artiodactyla the presence of camels¹¹ (*C. thomasi*) in Palæolithic Pleistocene times and even in deposits of Neolithic age (*C. dromedarius*) is extraordinarily interesting. There is no evidence as to domestication. The earlier of these two camels of ancient Libya had longer legs and was of heavier build than the dromedary. The rare remains of the later form, probably identical with the recent dromedary, may be those of a race which was already emigrating or becoming extinct. The presence of the camel is one of the most convincing proofs of connection of this fauna with that of the Upper Siwaliks of southern Asia, and thus of North America.

Especially significant of Asiatic and Siwalik affinity are the Pleistocene cattle and buffaloes of north Africa, including contemporary species of *Bos*, all belonging to late Quaternary or to the Neolithic age, partly domesticated, and with remote resemblances to the Pleistocene cattle of France and Spain. Similar Asiatic affinity is found in the remains of a buffalo (*Bubalus antiquus*) allied to the existing Indian form; this was a powerful beast which presumably lived in herds, frequenting grassy plains and swampy districts, and in its presence here we seem to find confirmation of what geology teaches us in regard to the dampness of the Quaternary climate. The disappearance of the buffalo from north Africa at the commencement of the Recent Period was no doubt due to the increasingly dry conditions, and partly to destruction by man.

The great number and variety of antelopes is most astonishing in this region, which at present is inhabited only by the gazelles (*Gazella*), the hartebeests (*Bubalis*) and addax antelopes (*Addax*). The Pleistocene fauna includes gnus (*Connochætes*), several species of *Bubalis* still represented in the Barbary States, an aberrant form (*Oreonagor*), related to the nilgai of India, nine species of gazelles (*Gazella*), the oryx (*Oryx*), the nabor (*Cervicapra redunca*), several large elands (*Oreos*), such as now inhabit south Africa, as well as dwarf antelopes (*Cephalophus*). Beside these plains and desert types of ruminants, the hills were covered with wild sheep (*Ovis palæotragus*) very similar to the existing Barbary sheep, as well as goats (*Ovis promaza*).

¹¹ POMEL, A.: "Caméliens et Cervidés." Carte Géol. Algérie. Paléont. Monogr. Algiers, 1893.

In the rivers there lived in early and later Pleistocene times a series of species of hippopotami (*H. hipponensis*, *H. sirensis*, *H. icosiensis*) leading to a form (*H. annectens*) related to the existing Nile hippopotamus. There are also two types of wild boar (*Sus*), and more abundant than these were the wart-hogs (*Phacochoerus*) found in the caves and alluvial deposits of Barbary.

Preying upon these Herbivora were lions, leopards and hyænas, which are compared by Pomel with Pleistocene cave forms of Europe. There are also jackals, wolves, the ichneumon and, possibly, a polecat.

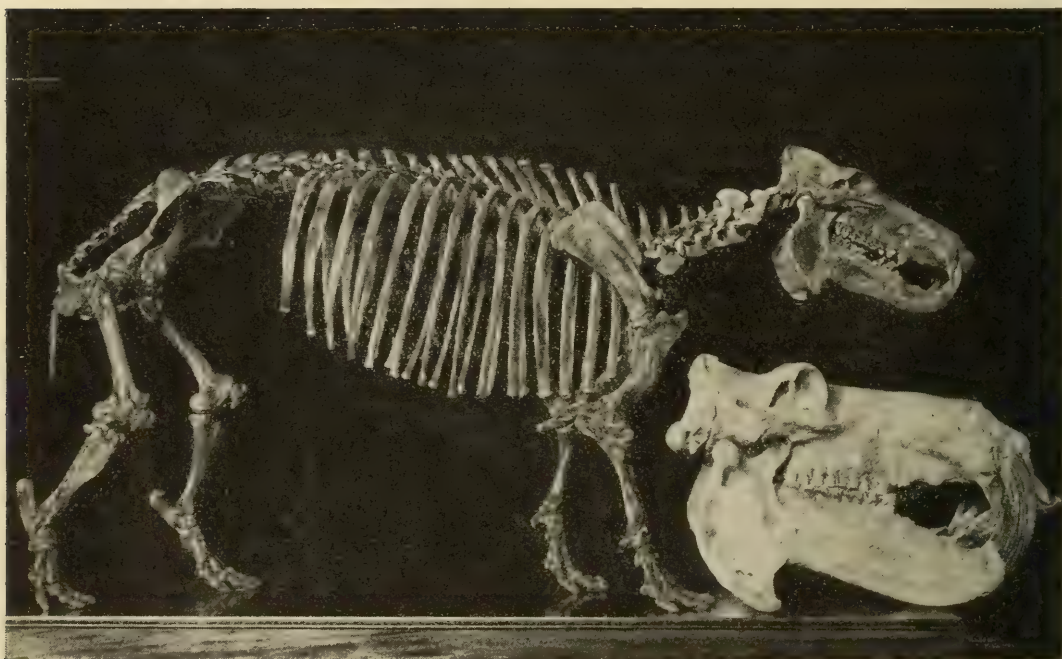


FIG. 2.—Skeleton of the Pleistocene pigmy hippopotamus of Madagascar, *Hippopotamus madagascariensis*, together with a skull of the recent hippopotamus, *H. amphibius*

In the American Museum of Natural History.

African-European Distribution.—Of this imposing list the following types occur both in Africa and in the Lower and Middle Pleistocene of Europe, the species being similar if not in some instances identical.

Southern elephant (*E. meridionalis*), which is also found in Pliocene and early Pleistocene deposits of Europe.

Elephants similar to *E. antiquus* of Europe and its dwarf representatives in Malta and other Mediterranean islands are found in the Upper Pleistocene deposits of north Africa.

Long-headed rhinoceroses. It would appear probable that the woolly rhinoceros (*D. antiquitatis*) which is closely related to the "white" rhinoceros (*D. simus*) originated in Africa, but no animal resembling it has been discovered in the African Pleistocene.

One of the Pleistocene horses of north Africa (*E. numidicus*) is closely similar to the Upper Pliocene *E. stenonis* of Europe.

With these animals may have come the lion (*Felis leo*) which was widely spread over southern Europe.

Hyænas. The striped (*H. striata*) and spotted hyænas (*H. crocuta*) are common to Europe.

Bears. The bear (*Ursus lybicus*) found fossil in Algeria seems to belong to the *Helarctos* group, possibly derived from the small *U. etruscus* of the European Pliocene and now represented by the Malayan sun bear.

Machærodonts. Recently (Stromer) sabre-tooth tigers have been discovered in Pleistocene Egypt.

Primates. The primates are represented by the macaque (*Macacus*), not very different from the existing forms which frequent the region of the Straits of Gibraltar. In Pleistocene times the macaques ranged northward into southern France (Harlé).

Suillines. Wild boar (*Sus*) may have affinities with the Pliocene types of Europe.

With the exception of the above list, there is little in common between the large fauna of north Africa and that of Europe in Pleistocene times.

AFRICA IN PALÆOLITHIC AND NEOLITHIC TIMES.

Giraffes very similar to the recent African giraffe (*C. giraffa*) have been found in mid-Pleistocene deposits associated with Palæolithic stone implements of the Chellean type.¹² Industry¹³ similar to the Chellean but not necessarily of the same age is found in Africa from Egypt to the Cape. Giraffes are also depicted in rock drawings of Neolithic age in Algeria.

In Neolithic times there existed at least one species of deer, whereas at present there are two kinds of deer, the red and the fallow,¹⁴ in north Africa, both undoubted Eurasiatic migrants.

The prehistoric men of the Barbary States apparently obtained and domesticated the horse, species of sheep and several dogs, and left many sketches of animals on the rocks of the region.¹⁵

PLEISTOCENE OR GLACIAL EPOCH IN EUROPE

After the establishment of the single glacial theory by Charpentier and Louis Agassiz (1836-1840), there gradually developed in Europe and

¹² PALLARY, P.: "Note sur la Girafe et le Chameau du Quaternaire Algérien." Bull. Soc. Géol. France, Ser. 3, Vol. XXVIII, pp. 908-909. 1900.

¹³ OBERMAIER, HUGO: "Der Mensch der Vorzeit. Band I. of Der Mensch aller Zeiten." Alleg, Verlags-Gesellsch. m. b. h. Berlin, Munich, Vienna, 1912.

¹⁴ See LYDEKKER, RICHARD: Deer of all Lands. The North African red deer (*Cervus elaphus barbarus*) is smaller than the European race. Evidence on the range of the common fallow deer (*Cervus dama*) in northwestern Africa is not very full.

¹⁵ See POMEL, '93, '94, '95, '96, '97, '98.

America the hypothesis of several glacial advances of varying duration and severity alternating with interglacial temperate periods during which the ice retreated and conditions of climate prevailed which in some instances were even milder than the present in the same latitudes.

As early as 1856 Morlot observed a relatively warm flora between two Swiss glacial deposits at Dürnten, and he subsequently advanced a theory of three glacial stages. James Geikie (1871-1894) developed the hypothesis of a succession of six glacial and five interglacial stages and climates. In 1883 Boule from his observations along the Mediterranean coast main-



FIG. 3.—Glacial map of northern Germany and the Netherlands

This map shows the drift and terminal moraines of Glaciations I-II, *Scanian + Saxonian* (old drift), III *Polandian = Riss* (middle drift), IV *Mecklenburgian = Würm* (upper drift). After Leverett, 1910.

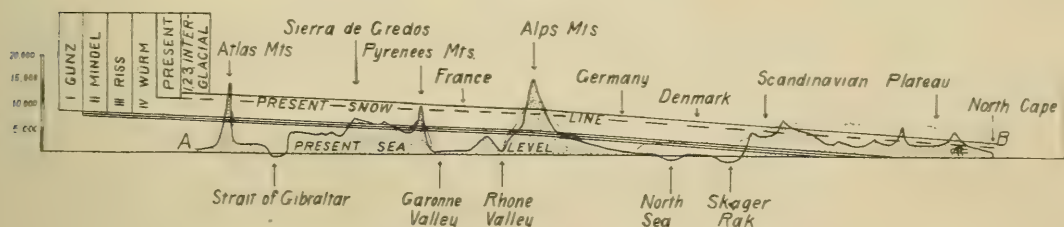
tained that there is evidence of three great glacial advances, the first falling within the close of the Pliocene Epoch, the second falling properly within the Pleistocene. The firm foundation of the quadruple theory in Europe was laid, however, by the researches of Penck and Brückner¹⁶ in the Alpine region, published in 1909. According to this classic work the entire Glacial Epoch is assigned to the Pleistocene or Quaternary Period. Its deposits include the entire "Diluvium" and "Drift" of earlier geologists.

All the river gravels, boulder-clays and moraines of the Glacial Epoch

¹⁶ PENCK, ALBRECHT, and BRÜCKNER, EDOUARD: *Die Alpen im Eiszeitalter. III. Die Eiszeiten in den Sudalpen und im Bereich der Ostabdachung der Alpen.* Leipzig, 1909.

are of later date than the marine Pliocene deposits of southern Europe. Before any of these glacial deposits occurred there was an elevation of the marine Pliocene strata along the southern Alpine borders from sea level to a height of from 300-500m.; there also occurred erosion of these marine strata by rivers. Thus in the valley of the Po there is a considerable time interval between the closing marine conditions of the Pliocene and the opening Pleistocene conditions. In the valley of the Rhone also there is a marked interruption between the strata of the Pliocene and of the Glacial epochs, the latter overlying the strata recognized as Upper Pliocene, which in turn overlie the marine Pliocene.¹⁷

This interval between the Pliocene and Pleistocene corresponds with very important changes which occur in the mammalian life of Europe, namely, in the extinction of many characteristic Pliocene mammals, such as the anthropoid apes, the antelopes and the mastodons.



PROFILE OF PAST AND PRESENT SNOWLINES AND GLACIERS OF EUROPE

FIG. 4.—Theoretic snow levels during the Glacial Epoch

Prepared under the direction of the author by Chester A. Reeds from data given by J. Geikie, Penck, Brückner, Leverett and Stieler's Hand-Atlas, December, 1914.

The traces of four different glacial advances and retreats observed around the northern slopes of the Alps by Penck and Brückner¹⁸ were followed with their "river drifts" and moraines down the Danube to the neighborhood of Vienna; they were found to be clearly marked in the region of the upper Rhine and of the Rhone around Lyons, and distinguishable both by the greater or the less extension of their borders and by the greater or less erosion which has occurred in the intervals between their successive depositions. These four advances were named respectively the Günz, the Mindel, the Riss and the Würm.

As an instance of the disparity between the duration of these several glacial advances with the accompanying descent of the ice and snow line, the old moraines of the Riss or third glaciation form a girdle around the more recent Würm or fourth glaciation, proving that the Riss was not

¹⁷ *Op. cit.*, pp. 654-655.

¹⁸ *Op. cit.*, p. 47.

only a more extensive glaciation but that the snow line was 100m. lower. It is also estimated that the climate of the Riss was one-twelfth more severe than that of the Würm.

In northern Germany only three great glacial advances are recorded, while still farther north, in Scandinavia, there was in a sense only one Glacial epoch, since the ice cap never retreated so far as to permit of interglacial deposits. This is in accordance with the anthropological fact that only toward the close of Postglacial times does Scandinavia show traces of human habitation in the arrival of the Neolithic men; whereas in France and Germany there is evidence of human habitation as early as the Second and Third Interglacial Stages.

In the meantime American geologists have also discovered similar proofs of four successive glacial advances and more temperate interglacial stages. The correlation of these conditions in the New and Old Worlds suggested by Penck, Chamberlin and others has recently been reviewed with great precision by Leverett,¹⁹ to whose work we shall frequently refer. The most recent results of geologic and anthropologic correlation with some original modifications are graphically presented in the accompanying diagram (Fig. 5) by the author and Reeds.²⁰

The river terraces are of great importance both in geology and in anthropology. In general the "high terraces" belong to the earlier glaciations and the "low terraces" to the latest. Thus the "high terraces" of the Alpine region belong to the Riss or glaciation III; in the valley of the Rhine the "high terrace" is visible near Bâsle; the "low terrace" of the Würm or glaciation IV occupies vast surfaces on the upper Rhine and contains a mammoth (*E. primigenius*) fauna. The "high terraces" in the Paris basin reach 30m. above the level of the Seine, while the "low terraces" are only 5m. above the level of the Seine and subject to floods; the "high terraces" in the valley of the Seine contain the First Interglacial (*E. meridionalis*, *E. stenonsis*) fauna, while the "low terraces" of the Seine and of the Somme contain the Second and Third Interglacial fauna (*E. trogontherii*, *E. antiquus*, and *D. merckii*).

DURATION OF THE PLEISTOCENE

The Pleistocene was estimated by the American geologist Dana (1874) to be equal to about one-fourth of the entire Cænozoic Era, *i. e.*, 700,000 years. By Ward (1885) and Williams (1895) it has been estimated at

¹⁹ LEVERETT, FRANK: "Comparison of North American and European Glacial Deposits." *Zeitschr. f. Gletscherkunde*, Vol. iv, pp. 241-316. 1910.

²⁰ REEDS, CHESTER A.: Dr. Reeds has prepared the climatic curve from data furnished by Penck, Leverett, Taylor, Chamberlin, Salisbury, Geikie, Schmidt, Coleman and Osborn. Dated October, 1914.

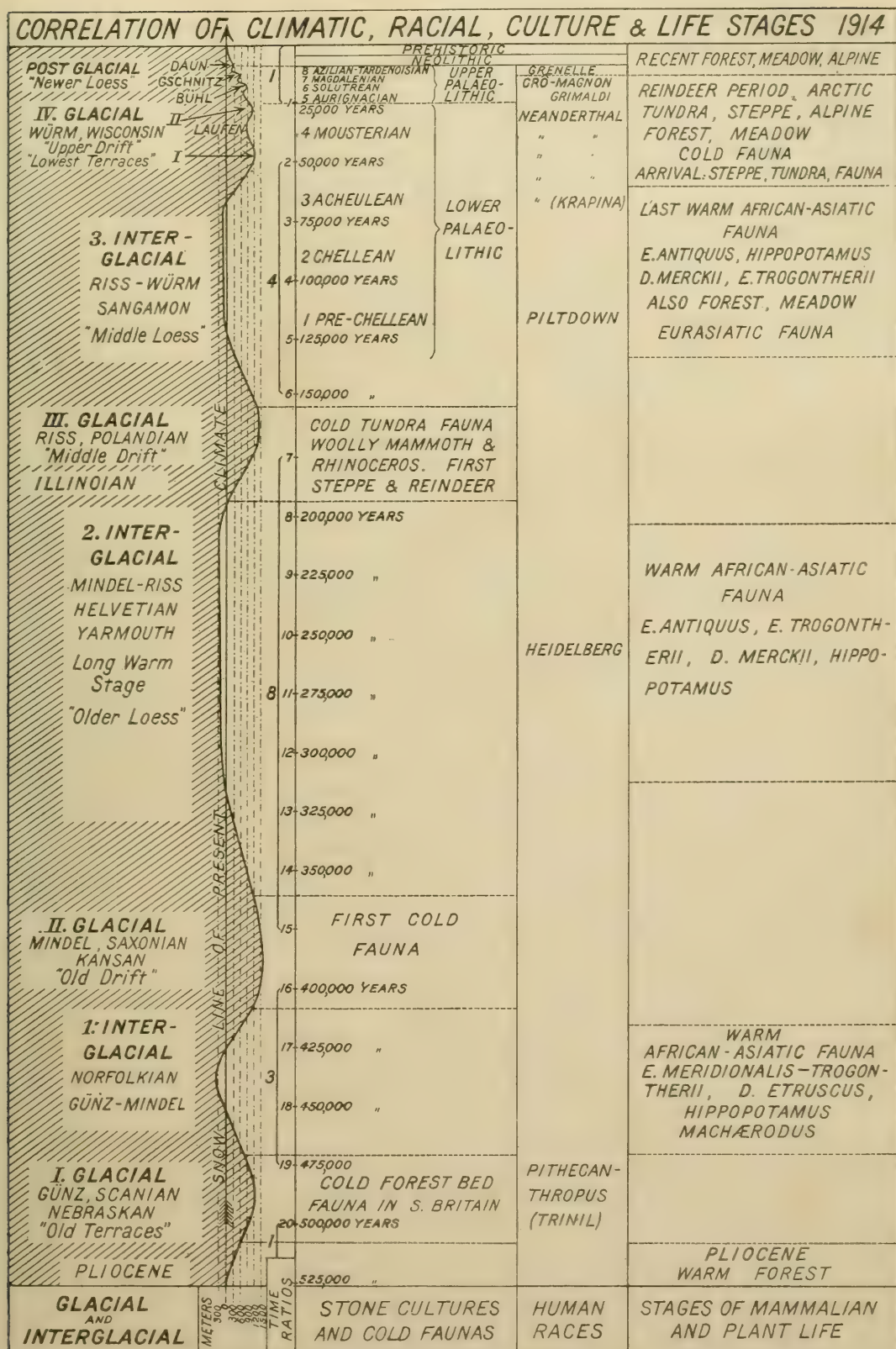


FIG. 5.—Divisions and contemporaneous events of the Glacial Epoch

Prepared under the direction of the author by Chester A. Reeds from data observed and correlated by J. Geikie, Penck, Chamberlin, Salisbury, Leverett, Schmidt, Coleman and Osborn. October, 1914.

TABLE II.—Time Estimates of Glacial and Interglacial Stages Adopted in this Volume

Glacial Stages, Snow Advances, Low Temperatures and Humidity	Relative Time Estimates	Human Culture Stages	Interglacial Stages, Snow Retreats, Higher Temperatures
DAUN	4, 000–5, 000 7, 000 16, 000–24, 000	Age of Copper	Postglacial 20, 000 to 34, 000 <i>Achen</i> retreat
GISCHNITZ		Neolithic	
BÜHL		Azilian	
		Magdalenian	
		Solutrean	
		Aurignacian	
IV Fourth Glacial, Würm	20, 000	Mousterian	<i>Laufen</i> retreat
I Maximum			
		Acheulean	Third Interglacial, Riss-Würm 60, 000–100, 000
		Chellean	
		Pre-Chellean	
III Third Glacial, Riss	20, 000		
		Heidelberg Race	Second Interglacial, Mindel-Riss 240, 000–400, 000
II Second Glacial, Mindel	20, 000		
			First Interglacial, Günz-Mindel 100, 000–160, 000
I First Glacial, Günz	20, 000		
			20, 000

one-third the entire Cænozoic, *i. e.*, 1,000,000 years. If with Wallace we accept Croll's theory and estimate, the last glacial advance would date back to the last period of great eccentricity of the earth's orbit, namely, 200,000 years, but this we now consider excessive. The following figures show the variations of opinion on this subject and the two opposite tendencies of greatly expanded or greatly abbreviated estimates of Pleistocene time:

Lyell, "Antiquity of Man".....	1863	800,000 years
Upham	1893	100,000 "
Walcott	1893	400,000 "
Sollas	1900	400,000 "
Penck	1909	520,000 to 840,000 years

The very high estimate of 840,000 years made by an eminent and usually conservative authority such as Penck appears excessive unless we are to expand our estimates of Tertiary time (see p. 63) to 20,000,000 years and of the pre-Tertiary into hundreds of millions of years.

All the arguments for the briefer estimates of Pleistocene time have recently been brought together by Wright.²¹

Antiquity of Man.—Vast interest attaches to this duration problem in connection with the antiquity of man. In the calculations of Penck²² the time since the Fourth or Würm glaciation has been used as a measure-unit to calculate the length of the previous glacial and interglacial periods. It is believed that since the climax of the Würm glaciation from 20,000 to 34,000 years have elapsed. Geologic, prehistoric and historic events since the close of the last glaciation make this estimate appear not excessive. In regard to the previous time intervals, the author does not pretend to give an absolute age estimate, but simply a survey of the relative magnitude of the time periods with which we are dealing.

The unit of measurement is Postglacial or post-Würm time which Penck²³ estimates at 20,000 years. On the basis of this estimate the time (520,000 years) covered by the whole Glacial Epoch is *relatively* distributed as follows:

²¹ WRIGHT, G. FREDERICK: *The Ice Age in North America and its Bearings upon the Antiquity of Man.* 8vo. Bibliotheca Sacra Co. Oberlin, 1911.

²² PENCK, A.: "Das Alter des Menschengeschlechts." *Zeitschr. Ethnol.*, No. 3, pp. 390-407. 1908.

²³ PENCK, A., and BRÜCKNER, EDOUARD: "Die Alpen im Eiszeitalter. Dritter Band. Die Eiszeiten in den Sudalpen und im Bereich der Ostabdachung der Alpen." 8vo. Tauchnitz, Leipzig, 1909. (pp. 1153-1176, "Chronologie d. Eiszeitalters in d. Alpen." Penck.)

	<i>Units</i>	<i>Relative duration Years</i>	<i>Totals Years</i>	<i>Descent of snow line. Meters</i>
Postglacial, post-Würm hemicycle...	1	20,000	20,000
IV or WÜRM GLACIATION.....	1	20,000	40,000	1,200
3rd or Riss-Würm Interglacial Stage.	3	60,000	100,000
III or RISS GLACIATION.....	1	20,000	120,000	1,250
2nd or Mindel-Riss Interglacial Stage	12	240,000	360,000
II or MINDEL GLACIATION.....	1	20,000	380,000	1,300
1st or Günz-Mindel Interglacial Stage	5	100,000	480,000
I or GÜNZ GLACIATION.....	1	20,000	520,000	1,200

The three chief conclusions of Penck are as follows:

1. If the whole Ice Age extended over a period of 500,000 to 1,000,000 years, the Second very long warm Interglacial Stage, also known as the Mindel-Riss or Helvetian, is reckoned at more than 200,000 years, while the final relatively short interglacial stage, the Riss-Würm, is reckoned at 60,000–100,000 years.

2. The duration of the Lower Palæolithic culture periods, the pre-Chellean, Chellean and Mousterian, would by this reckoning be much longer than that of the Upper Palæolithic culture periods, the Aurignacian, Solutrean and Magdalenian. Penck estimates that since the beginning of Magdalenian times 24,000 years may have elapsed and since its close about 16,000 years.

3. Compared with these prolonged Palæolithic divisions the Neolithic Stone and Metal periods have occupied an almost unappreciable length of time. If the beginning of the Neolithic lake dwellings is dated about 5,000 to 7,000 years ago we estimate that the beginning of the Copper Age in Europe dates back between 3,000 and 3,500 years; in Africa it is much more ancient.

The human culture stages are arranged above not according to Penck but according to the more recent correlations of Obermaier, Breuil, Schmidt and others.

GEOLOGIC AGE OF THE CULTURE STAGES

The trend of Palæolithic research lately has been to draw all the human culture periods from the pre-Chellean to the Magdalenian closer together and to reduce the time assigned for their evolution. All the French authorities, led by Boule, Cartailhac, Breuil and Obermaier, are now agreed in assigning the earlier Palæolithic cultures, the pre-Chellean, Chellean and Acheulean, to the Third Interglacial Stage and not to the Second. Schmidt has also lately declared himself in favor of this view after a most exhaustive and valuable investigation of this problem.

A summary of the correlation presented in this chapter is embodied in the Table of Osborn and Reeds above. A summary of the very diverse opinions on this subject is embodied in the Table of Wieggers below.

A very strong reason for abbreviating our estimates of the period which has elapsed since the appearance of man of the pre-Chellean culture stage in Europe is found in the relatively unchanged condition of the river valleys of the Somme in northern France and of the Vézère in Dordogne, in which the earliest human cultures occur. The Vézère has not materially changed since Acheulean times. The pre-Chellean, Chellean and Acheulean specimens found in the Somme valley are also connected with the present river system. Both on the Somme and the Marne the Chellean and pre-Chellean cultures occur on the "lowest terraces." Again, there is no faunal break between late Chellean and early Acheulean times nor between late Acheulean and early Mousterian times. The first great faunal break is that produced by the Fourth glaciation.

In favor of Penck's contention as to the earlier geologic age of the Chellean is the occurrence of pre-Chellean and Chellean palæoliths in association with a very primitive mammalian fauna such as is characteristic of Second Interglacial times.

ELEVATION AND SUBSIDENCE OF LAND IN QUATERNARY TIMES

The relations of the mammals of Europe with those of Asia on the east and Africa on the south were profoundly affected in Pleistocene times by the periods of elevation of the continental shelf, resulting in the creation of new land connections which facilitated migration, or of subsidence which cut off and isolated many migrating forms from their centres of origin and dispersal. The maximum elevation, as represented in the accompanying diagram (Fig. 1), never occurred in all portions of the continent of Europe at the same time, because there were oscillations both on the northern and southern borders of Europe and Asia.

The beginning of the Pleistocene Epoch is one of elevation and is remarkable for the broad land connections between Europe, Africa and Asia. It represents the last stage in that vast community of mammalian life which during Pliocene times distinguished the entire region of Europe, Asia and Africa.

The theoretical relation which elevation and subsidence respectively bear to the glacial and interglacial stages and phenomena is, broadly speaking, as follows:

ELEVATION, emergence of the land from the sea, broad land connections facilitating migration, retreat of the ice caps, periods of erosion of the river valleys and formation of terraces.

TABLE III.—Correlation of Archaeology and Glaciology by Different Authors

Geological Divisions	Obermaier, 1912	Schmidt, 1912	Penck, 1910	Bayer	Wiegiers, 1913	
Postglacial	Magdalénien Solutréen Aurignacien	Magdalénien Solutréen Aurignacien	Magdalénien	Magdalénien	Metalzeit Jüngere Steinzeit Campignien Azilian	Mya-Zeit Litorina-Zeit } Ancylus-Zeit
IV Glacial	Moustérien	Moustérien	Solutréen	Jung-Solutréen	Magdalénien Solutréen Aurignacien Moustérien II	{ Bühlstadium Yolda-Zeit bzw. } Postglazial { Hochglazial } Frühglazial
3rd Interglacial	Moustérien Ältestes Kalt: Acheuléen Warm: Chelléen	Acheuléen Chelléen	Moustérien	Alt-Solutréen Aurignacien Steppenphase Moustérien Gemässigte Waldphase.	Moustérien I	—
III Glacial	—	—	Moustérien	Kaltes Moustérien	Acheuléen II	—
2nd Interglacial	—	—	Kalt: Acheuléen Warm: Chelléen	Acheuléen Chelléen	Acheuléen Chelléen	—
II Glacial	—	—	—	—	} Prächelléen	—
1st Interglacial	—	—	—	—		—

Various correlations of geologic and palæolithic culture stages. See: WIEGERS, SCHUCHHARDT, HILZHEIMER. "Studienreise zu den paläolithischen Fundstellen der Dordogne." Discussion: GAGEL, WIEGERS, SCHUCHHARDT, WIEGERS. Zeits. f. Ethn., Jahrg. 45, Heft I, pp. 126-154. 1913.

SUBSIDENCE, submergence of the land and advance of the sea, land connections interrupted, advance of the glaciers, periods of deposition and filling of the valleys.

Thus Boule and Geikie consider the glacial stages as mainly periods of continental subsidence and filling of the valleys, the interglacial as times of elevation and erosion of valleys and terraces. Penck estimates the elevation of southern Europe at 100m. in the beginning of Pleistocene times; he speaks of the elevation of the Alps during the Second Interglacial Stage. Geikie describes the southern half of the North Sea as dry land during the First Interglacial Stage traversed by a northern extension of the River Rhine, while the approach of the Second Glacial Stage was heralded by a submergence of this area of the North Sea. Again (Geikie) during the Second Interglacial Stage the English Channel and probably a large part of the North Sea became dry land. Finally (Pohlig) during the Third Interglacial Stage there was a period of continental elevation and a dry, cold steppe climate in western Europe.

Consistent with this hypothesis is the deposition of loess during the Second and Third Interglacial Stages, also during the Postglacial Stage, because loess deposition is characteristic of dry and elevated continental climates with winds prevailing in one direction.

Final Subsidence.—Consistent with this hypothesis also is the fact that general and local *subsidence* in the northern hemisphere was the chief feature of closing Pleistocene times or the very cold Postglacial Stage; all the old continental connections which had been characteristic of the Tertiary were cut off; in the northwest the English Channel was formed, Great Britain became isolated from Europe, Ireland first lost its land connection with Wales and then with Scotland; to the eastward the Mediterranean Sea extended into the Ægean region and cut off the old land connection between Greece and Asia, which had so long served to connect Greece with the mammalian life of southern Asia. During a period of extreme subsidence, the Black Sea, the Caspian, the Sea of Aral formed a large single sheet of water known as the Hyrcanian Sea. In southern Asia similar subsidence and separation phenomena were in progress; the islands of the East Indies, Sumatra and Java were cut off from the Malay Peninsula. The separation of the Japan and Philippine archipelagos probably occurred in late Postglacial times. To the far north-east late in Pleistocene times Asia lost its connection with America, Bering Straits were reopened, and the so-called Nearctic region of North America was completely isolated from the Palæarctic region of Eurasia after a long period of community and free intermigration of Holarctic life.

Final Elevation.—This extreme subsidence was followed in late Post-glacial times both in Europe and America by reëlevation which gave the continents their present contours and climates.

ALTERNATIONS OF CLIMATE AND FLORA

Fluctuations of temperature and of moisture in Pleistocene times are indicated first by the advances and retreats of the ice caps, second by the presence of arctic or temperate Mollusca in the coast waters, third by the variations in the flora in glacial and interglacial times, fourth by the alternate appearance of the northerly or southerly types of mammals and birds, fifth by the nature of the geologic depositions, sixth by the nature of the land Mollusca in the loess. Combining the evidence derived from these various sources the theoretic broad divisions of the climatic sequence are as follows: (1) the cold and moist phases connected with the successive glacial advances and retreats; (2) the warm to temperate climates of the First and Second Interglacial Stages and first half of the Third Interglacial; (3) the dry and cold climate of the second half of the Third Interglacial Stage and early Postglacial times; (4) the damp and cool climate of late Postglacial times favorable to forests.

The theoretic alternating conditions of each complete glacial cycle are as follows:²⁴

Subsidence:	Glacial Maximum:	Tundra flora and fauna
	Glacial Retreat:	Cool and moist forest flora and fauna
Elevation:	Interglacial:	Dry conditions, flora and fauna. Steppe
	Glacial Advance:	Cool forest fauna and flora
Subsidence:	Glacial Maximum:	Cold tundra flora and fauna

Low Glacial Stage Temperatures.—Low temperatures during the periods of glacial advance are attested both by the advent of northern Mollusca, marine and terrestrial, northern flora, and the repeated arrival in Europe of members of the cold fauna of the arctic tundras, including both the smaller and the larger mammals and the birds, as well as the cold fauna of the high, arid steppes of western Asia. Low temperatures are attested also in early Postglacial times during the great Aurignacian-Magdalenian art period by the heavy covering of hair indicated on all the animals depicted by the Upper Palæolithic artists. This hairy covering coincides exactly with that of the extreme northern tundra types of reindeer, woolly rhinoceros (*D. antiquitatis*) and woolly mammoth (*E. primigenius*) found imbedded in the ice or frozen soil.

²⁴ Compare Wüist.

Moderate Estimates of Temperature.—That the advancing glaciers alone do not constitute proof of very low temperatures is observed in Alaska, where very heavy snowfall or precipitation causes the accumulation of great glaciers, although the mean annual temperature of the glacier region is 40° – 45° F. (4.44° – 7.22° C.) as compared with that of northern Germany, 45° – 50° F. (7.22° – 10° C.), *i. e.*, from mouth of Rhine S. E. along source of northward flowing rivers, *e. g.*, Elbe, Vistula, etc. Neumayr estimated that during the Ice Age there was a general lowering of temperature in Europe of not more than 6° C., and held that even during the glacial advances a comparatively mild climate prevailed in Great Britain. Martins estimated that a lowering of temperature to the extent of 4° C. would bring the glaciers of Chamonix down to the level of the plain of Geneva. Penck estimates that all other atmospheric conditions remaining the same as now a fall of temperature to the extent of 4° to 5° C. would be sufficient to bring back the Glacial Epoch in Europe. Perhaps the strongest proof that Europe was not refrigerated during the first, second and third glacial advances is the survival of the African-Asiatic fauna throughout the whole period until the fourth glaciation, which was accompanied by widespread severity of climate.

Warm and Temperate Interglacial Stages.—Similarly the early hypotheses of extremely warm or subtropical conditions, based chiefly upon the northerly distribution of hippopotami and rhinoceroses, animals which we now associate with tropical conditions, are not supported by the study of the interglacial flora. It is quite probable that both the hippopotami and rhinoceroses of the so-called "warm fauna" were covered with hair although by no means so thickly covered as the woolly rhinoceros and elephant of the arctic tundras. There is evidence that in the First Interglacial Stage southern England and France enjoyed somewhat warmer and moister conditions of climate than the present. The Second Interglacial Stage also, which is commonly distinguished as the "long warm" Interglacial Stage, was of somewhat higher temperature than the present. The general evidence is that both in Europe and North America, especially in the First and Second Interglacial intervals, the climate in the northern hemisphere was somewhat more equable and milder than at present, with a higher mean temperature, at certain intervals with greater precipitation of moisture, at other intervals much more cool and arid. There was perhaps more sunshine than now.

As a result of favorable interglacial conditions arboreal vegetation flourished to the far north along the Arctic ocean, and the present tundra regions of Siberia and British America then supported forests which

have long since been extirpated, the northern limit of similar living trees now lying far to the south.

Alternations of Flora.—It is clear from these great successive fluctuations of temperature, moisture and aridity during Pleistocene times that the flora cannot be treated as a unit nor as progressing in a single direction like the flora of preceding epochs; the flora as well as the fauna presented alternations of arctic, boreal and temperate species which migrated southward and northward following the advances or retreats of the glacial cap. Thus we may observe evidences of changes of climate and flora from forested conditions to steppe conditions and back to forested conditions. From the beginning of the Fourth Interglacial interval to the present time, the Alps region (Penck, Brückner, 1909) has apparently gone through a cycle of changes such as the following:

VEGETATION	CLIMATE	EPOCH
Fourth, forest conditions	Western European, oceanic	Modern
Third, steppe conditions	Western Asiatic, continental	Fourth Glacial and Postglacial
Second, tundra conditions	Northeastern-European, subarctic	Fourth Glacial
First, forest conditions	Western-European, oceanic	Third Interglacial

The elephants (Hilzheimer, 1913) in the structure of their grinding teeth afford clear indications of the plant life, whether consisting mainly of grasses or forests, but not of climate except in so far as vegetation is dependent upon moisture. The advance and retreat of the ice is dependent both upon moisture and extreme cold and involves the frozen subsoil conditions of the tundras which are fatal to forests. Cases of alternation of conditions favorable to *Elephas trogontherii*, which is believed to be a grass-eating form, and of *Elephas antiquus*, which is believed to be a forest-living form, are observed in Taubach by Wüst.²⁵ This author observes in the lower layers *Elephas antiquus* succeeded in the middle layers by *E. trogontherii* and then in the upper layers again by *E. antiquus*, and deduces from this succession a change of conditions from forest, to steppe, to forest.

FAUNAL LIFE ZONES OF EUROPE

In the whole history of the Mammalia in various parts of the world we know of no conditions so unusual and complex as those which prevailed in Europe in Pleistocene times. These conditions were the product of

²⁵ WÜST, EWALD: "Die plistozenen Ablagerungen des Travertingebietes der Gegend von Weimar und ihre Fossilienbestände in ihrer Bedeutung für die Beurteilung der Klimaschwankungen des Eiszeitalters." Zeitschr. Naturw., Bd. 82, pp. 161-252. Leipzig, 1911.

cycles of environment and of life which have never prevailed before and will never recur even if the world were to enter a fifth glacial stage, for besides the extraordinary geographic and climatic changes which have been outlined in the previous pages there was the prodigal profusion of life which survived from Pliocene times and has since become extinct.

The result of these complex conditions was the assemblage in Europe of animals indigenous to every continent on the globe except South



FIG. 6.—Five chief zoögeographic regions of Europe, Asia and northern Africa from which the mammals migrated into western Europe during the Pleistocene

America and Australia, and adapted to every climatic life-zone from the warm and dry plains of southern Asia and northern Africa to the temperate forests and meadows of Eurasia, from the alpine heights of the Alps, Pyrenees and Altai Mountains to the high, dry steppes of central Asia with their alternating heat of summer and cold of winter, from the tundras or barren grounds of Scandinavia, northern Europe and Siberia to the mild climate of southern Europe. All these animals had been evolving during the Pliocene Epoch in these various habitats and they

also underwent a very considerable evolution during Pleistocene times in their respective habitats.

Owing to successive migrations and invasions into Europe of these exotic types of the north and south we should not expect to find a continuous phyletic evolution or transformation such as we have observed in the earlier epochs, excepting only that which occurred among the Eurasiatic forest and meadow types which appear to have been native or indigenous in Europe from the earliest Pleistocene to prehistoric times. These Eurasiatic forest and meadow mammals were continuous residents, retreating in the coldest periods to the shelters on the east and south. *Cervus elaphus*, for example, passed through several subspecific stages of evolution. The invading hordes from the tundras, the steppes, from northern Africa and from Asia represent branches which had their evolution elsewhere. This is true both of the mammals and of the races of men which had their genesis in the far east and southeast and arrived in Europe when it was a fertile peninsula, a region too small to be the seat of a continental evolution or adaptive radiation.

The five great regions which contributed to the European Pleistocene were as follows:

AFRICAN AND ASIATIC, PLAINS AND FOREST TYPES

EUROPEAN AND ASIATIC, FOREST AND MEADOW TYPES

EUROPEAN AND ASIATIC, ALPINE TYPES

STEPPE REGIONS OF SOUTHERN EURASIA AND EASTERN SIBERIA

ARCTIC TUNDRA REGIONS OF NORTHERN EURASIA

Literature.—The African-Asiatic element in these Pleistocene faunas was the first to be recognized and commented upon by the early writers; it is commonly known as the "warm fauna." We owe especially to Nehring the discrimination between the tundra and the steppe faunas. Gaudry, Harlé, Woldrich, Studer and Boule have added to our knowledge of these faunæ. Other contributors are Pohlig, Soergel, Förster, Hiltzheimer, Wüst and Dietrich. A strict systematic revision and introduction of the trinomial system is greatly needed. The most complete recent faunal lists of the late Pleistocene deposits in which traces of man are found are those of Koken and Schmidt (1912), who have also instituted the closest correlation between the migrations of the Mammalia and the successive stages of human culture.

African-Asiatic Mammals. Warm Fauna.—These mammals include those which first appear in the Upper Pliocene and survive into Lower Pleistocene times; also those which first appear in the Second Interglacial Stage and constitute the so-called "warm fauna" which survived in Europe until the middle or close of the Third Interglacial Stage. The

principal members of this list together with the probable continental centres of their origin are as follows:

<i>Macacus</i> ? sp. (Africa)		Macaque baboon
<i>Elephas meridionalis</i> (Asia)	Sudelefant	Southern mammoth
<i>Elephas antiquus</i> (Asia-Africa)	Altelefant	Straight-tusked elephant
<i>Dicerorhinus etruscus</i> (Asia)	Nashorn	Etruscan rhinoceros
“ <i>merckii</i> (Asia)	Mercksches Nashorn	Broad-nosed rhinoceros
<i>Hippopotamus major</i> (Asia)	Flusspferd	Hippopotamus
<i>Bos primigenius</i> (Asia)	Urochs, Auerochs	Urus
<i>Bison priscus</i> (Asia)	Wisent, “Auerochs”	Primitive bison
<i>Equus stenonis</i>		Upper Pliocene horse
<i>Machærodus latidens</i>		Sabre-toothed tiger
<i>Hyæna spelæa</i> (Asia-Africa)	Höhlenhyäne	Cave hyæna
“ <i>striata</i> (Asia-Africa)		
<i>Canis aureus</i> (Africa)	Schakal	Jackal
<i>Felis leo antiqua</i> (Africa)	Altlöwe	Lion
“ <i>pardus</i>	Leoparde	Leopard

The remains of these animals play a very important part both in the subdivision of the geologic horizons of Europe and in theories regarding the alternation of climates, as well as in the determination of the antiquity of man. They are found chiefly in the river sands, river deposits and “High Terraces” of the First and Second glaciations and “Low Terraces” of the Third Glacial and Interglacial Stages. Some survivors are found in the shelter and cavern deposits of the Third Interglacial Stage as objects of the chase. Only two of these animals, the urus and the bison, survive to become members of the Prehistoric Forest and Meadow Fauna of Europe. The lion also survived into Postglacial times but disappeared in Europe before the Prehistoric and Neolithic periods.

Although originally derived from southern Asia or from Africa, the woolly elephant (*E. primigenius*) and woolly rhinoceros (*Diceros antiquitatis*) are not to be placed with the African-Asiatic fauna because they appear in Europe only with the northern Glacial or Tundra Fauna and are invariably indicative of cold climatic periods.

Eurasiatic Forest and Meadow, Temperate Fauna.—These animals were resident in the forests and meadows of Europe during the entire Pleistocene Epoch and survived with a few exceptions into Postglacial and Prehistoric times. In fact, they are probably separable by differences of specific and subspecific value from their successors in prehistoric Europe, but many authors still embrace them within the existing specific terms. They are divided into Forest and Meadow types, the former with brachyodont teeth adapted to browsing habits and forest environment, the latter with elongate or hypsodont grinding teeth adapted to meadows and a diet

of grasses. Some of them, like the beavers, are stream- and river-dwellers. Naturally there is not always a sharp line of division between the habitats of these Forest and Meadow types: the Carnivora especially wander after their prey from the forests into the meadows and along the stream borders. The cattle and bison frequent both the forests and meadows.

FOREST MAMMALS

<i>Sus scrofa ferus</i>	Wildschwein	Wild boar
<i>Cervus elaphus</i>	Edelhirsch	Red deer, stag
<i>Megaceros Germaniæ</i>	Riesenhirsch	Giant deer
<i>Cervus maral</i> (Persia)		Maral deer
<i>Capreolus capreolus</i>	Reh	Roedeer
<i>Alces latifrons</i>	Elch	Moose (broad-faced)
<i>Equus mosbachensis</i>		Horse of Mosbach
<i>Trogontherium cuvieri</i>		Giant beaver
<i>Castor fiber</i>	Biber	Beaver
<i>Sciurus vulgaris</i>	Eichhörnchen	Squirrel
<i>Lepus cuniculus</i>	Wildkaninchen	Wild rabbit
<i>Arvicola amphibius</i>	Wasserratte	
“ <i>ratticeps</i>	Nordische Wuhlratte	
“ <i>agrestis</i>	Erdmaus	
“ <i>glareolus</i>	Rötelmaus	
<i>Myoxus</i>		Dormouse
<i>Mus sylvaticus</i>		Forest mouse
<i>Talpa europæa</i>		Mole
<i>Ursus deningeri</i>	Deninger Bär	
“ <i>arctos</i>	Brauner Bär	Brown bear
“ <i>spelæus</i>	Höhlenbär	Cave bear
“ <i>arvernensis</i>		Val d'Arno bear
<i>Felis catus</i>	gem. Wildkatze	Wild cat
<i>Lynx lynx</i>	gem. Luchs	Lynx
<i>Lynx cervaria</i>	Silberluchs	Eurasiatic lynx
<i>Canis lupus</i>	Wolf	Wolf
“ <i>neschersensis</i>		
“ <i>Suessi</i>		
<i>Vulpes alopex</i>	gem. Fuchs	Common fox
<i>Meles taxus</i>	Dachs	Badger
<i>Mustela vulgaris</i>	gem. Marden	Marten
“ <i>martes</i>	Edelmarder, Baum- marder	Pine marten
<i>Gulo luscus</i>		Wolverine
<i>Futorius putorius</i>	Iltis	Polecat
<i>Lutra vulgaris</i>	Fischotter	Otter

MEADOW MAMMALS

<i>Bison priscus</i>	Wisent	Bison
<i>Bos primigenius</i>	Urochs	Urus
<i>Equus caballus</i> (? sp.)		

<i>Factorius vulgaris</i>	Wiesel	Weasel
<i>Sorex vulgaris</i>		Shrew
<i>Cricetus vulgaris</i>		Hamster
<i>Arvicola terrestris</i>	Schermamus	
“ <i>arvalis</i>	gem. Feldmaus	Meadow vole

Of these forest-living animals the giant deer (*Megaceros*), the cave bear (*Ursus spelæus*), the Maral deer (*Cervus maral*), the giant beaver (*Trogontherium*) and the early Pleistocene species of horse are among

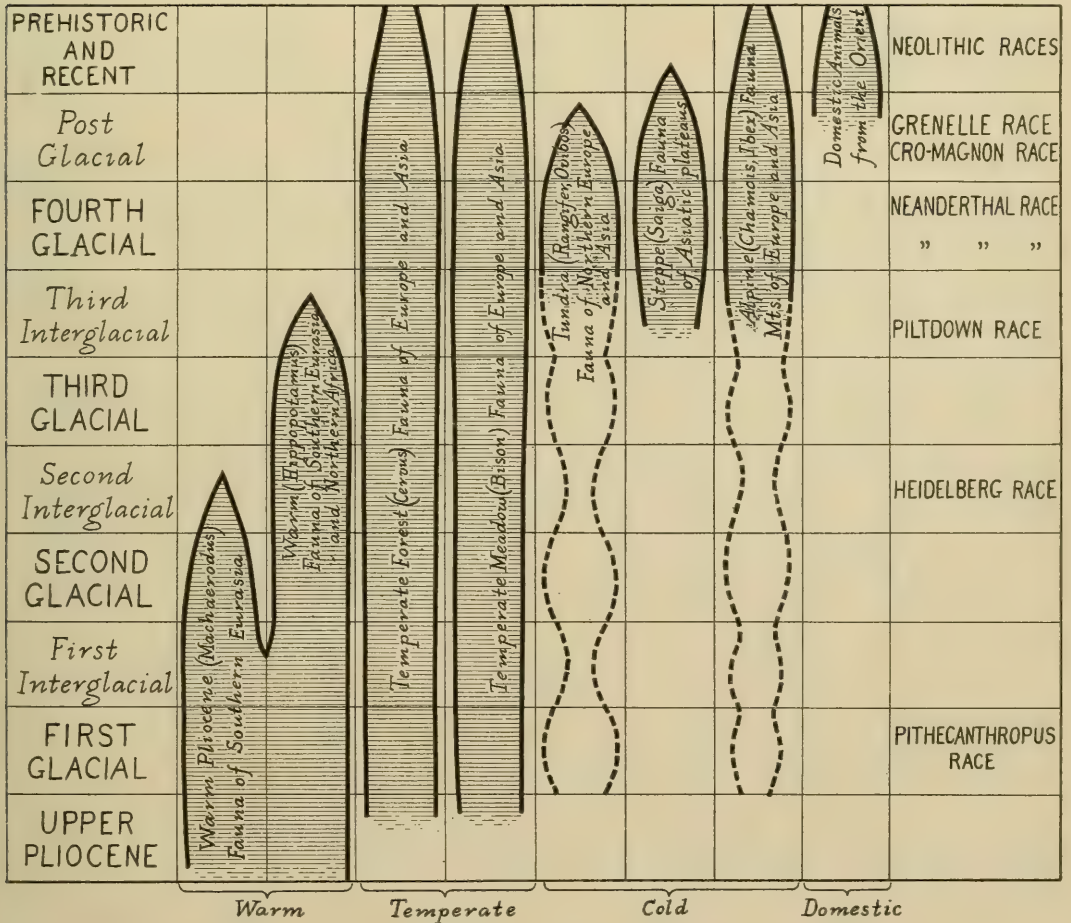


FIG. 7.—Introduction, succession and extinction of the faunæ from the five chief zoögeographic regions

African-Asiatic, Eurasiatic Forest and Meadow, Tundra, Steppe and Desert, Alpine.

the few forms which became extinct during the Glacial and Postglacial epochs. The great majority of these species survived with successive subspecific modifications.

It is a very remarkable fact that this true forest fauna of Europe is frequently found in the same deposits with the “warm fauna” of African-Asiatic origin. The bison and wild cattle appear in Europe from early

Pleistocene times, and in late Glacial and Postglacial times they occur as companions of the mammoth and the woolly rhinoceros.

Alpine Mammals, Cold Fauna.—During the severe conditions of late Pleistocene times the Alpine mammals were driven down into the plains or to the lower mountains and hills, and their remains occur principally during the last Glacial advance. They are represented both in the drawings and in the sculptures of the men of the reindeer or cave period.

<i>Ibex priscus</i>	Steinbock	Primitive ibex
<i>Rupicapra tragus</i>	Gemse	Chamois
<i>Ovis argaloides</i> (Altai Mts.)	Argalischaf	Argali sheep
<i>Arvicola nivalis</i>	Schneemaus	Alpine vole
<i>Lagopus alpinus</i>	Gebirgsschneehuhn	Ptarmigan

Steppe Fauna of Russia and Siberia.—Steppe conditions of climate were rendered possible in Europe by the elevation and extension of land much farther to the north and northwest than at present. At such periods all the tempering influences of the Atlantic Ocean were cut off from northern Europe and helped to give central Europe a cold, dry continental climate favorable to dust storms.

Boule, Kobelt²⁶ and Scharff²⁷ have agreed in the opinion that the presence of steppe mammals affords inadequate proof of steppe conditions in the country. Other authors (Hilzheimer, 1913), however, strongly sustain the steppe-climate theory. The evidence for steppe conditions of climate has been strengthened in recent years by the discovery of three successive loess deposits.

The steppe regions of eastern Europe around the Caspian Sea and of central Asia still maintain this highly characteristic steppe fauna. The climate is usually one of hot, dry summers with high winds and prolonged cold winters with sweeping snow storms. The animals are consequently very hardy. The fauna includes the jerboa, suslik, bobac marmot, dwarf pica, hamsters, northern voles, corsac fox, the manul, or Pallas's cat (*Felis manul*). Covering the plains are the larger grazing animals such as the saiga antelopes, wild asses and wild horses (including the *Equus przewalskii* type). Another animal which probably belonged to the Steppe fauna is the *Elasmotherium*.

<i>Elasmotherium sibiricum</i> ²⁸		Elasmothere
<i>Equus przewalskii</i>		Wild Gobi horse
“ <i>hemionus</i>	Dschiggetai	Dzeggetai, wild ass, kiang

²⁶ KOBELT, W.: Die Verbreitung der Tierwelt. Gemässigte Zone. Leipzig, 1902.

²⁷ SCHARFF, R. F.: The History of the European Fauna. London, 1899.

²⁸ GAUDRY, ALBERT, and BOULE, MARCELLIN: Matériaux pour l'Histoire des Temps Quaternaires. Trois. Fasc. L'Elasmotherium. 4to. Libr. F. Savy, pp. 83-104, pl. xvi-xix. Paris. 1876.

<i>Saiga tartarica</i>	Saiga antilope	Saiga antelope
<i>Alactaga jaculus</i>	Gr. Pferdespringer	Jerboa
<i>Lagomys pusillus</i>	Zwergpfeifhase	Dwarf pica, or tailless hare
<i>Spermophilus rufescens</i>	Rötliche Ziesel	Suslik, or pouched marmot
<i>Cricetus phæus</i>	Kl. Steppenhamster	Steppe hamster
<i>Arctomys bobac</i>		Bobac, or Polish marmot
<i>Myodes lagurus</i>		Steppe lemming
<i>Arvicola gregalis</i>	Sibirische Zweibelmaus	Steppe vole
<i>Canis corsac</i>		Corsac wolf
<i>Putorius evermanni</i>		Steppe weasel
<i>Tetrao tetrix</i>	Birkhuhn	Moorhen

*Tundra or Barren Ground Fauna and Flora.*²⁹—Certain members of the Tundra Fauna adapted to the long cold winters and short summers of the lands bordering the Arctic Ocean appeared in Europe at the height of each of the great glacial advances. The remains of these animals are always found within or close to the glacial drifts until the Fourth Glaciation when they spread all over France, Germany and Austria. Thus the musk-ox (*Ovibos moschatus*) is recorded in the (?) First Glacial advance of the Forest Bed of England. A tundra fauna including the reindeer (*Rangifer tarandus*) is recorded (Förster, 1913) with the Third Glacial advance (Upper Mauer sands). An extensive Tundra Fauna also appears with the Third Glacial, or Riss Stage, in the "Mammutlehm" of Cannstatt (Koken, Schmidt, 1912, p. 270); this is termed the "Older *Primigenius*" Fauna and occurs on the "high terraces" with the older Diluvium; it includes the woolly mammoth, the rhinoceros, the horse and the reindeer. The Tundra Fauna reappears toward the close of the Third Interglacial Stage (*i. e.* "Lower Rodent" layer), but the full series of species characteristic of the Tundra Fauna are not recorded in Europe until the Postglacial Stage (*i. e.* "Upper Rodent" layer), when the entire Tundra list given below is discovered either mingled with the culture remains of the Neanderthal race of men in Mousterian times or is represented in the art of the Crô-Magnon men of the reindeer period. The full or typical Tundra list of the Fourth Glacial Epoch is as follows:

<i>Elephas primigenius</i>	Mammut	Mammoth
<i>Diceros antiquitatis</i>	Wollhaariges Nashorn	Woolly rhinoceros
<i>Rangifer tarandus</i>	Ren	Barren ground reindeer
<i>Ovibos moschatus</i>	Moschusochse	Musk-ox
<i>Lepus variabilis</i>	Schneehase	Arctic hare
<i>Myodes obensis</i>	Oblemming	Obi lemming, or Siberian lemming

²⁹ NEHRING, A.: Über Tundren und Steppen der Jetzt- und Vorzeit, mit besonderer Berücksichtigung ihrer Fauna, pp. 81-166. Berlin, 1890.

<i>Myodes torquatus</i>	Halsbandlemming	Banded lemming
<i>Canis lagopus</i>	Eisfuchs	Arctic fox
<i>Gulo borealis</i>	Vielfrass	Wolverine (glutton)
<i>Fætorius erminea</i>	Gr. Hermelin	Ermine
<i>Arvicola nivalis</i>		Arctic vole
<i>Lagopus albus</i>	Moorschneehuhn	Ptarmigan
<i>Asio palustris</i>	Sumpfeule	
<i>Cygnus musicus</i>	Singschwan	

Animals like the banded lemming adapted to extreme northerly conditions generally cling to these very obstinately and perish rather than conform to an altered environment (Nehring). This species dwells immediately to the north of the region of coniferous forests, among scattered shrubs of the common juniper (*Juniperus communis*), the dwarf birch (*Betula nana*), the polar willow (*Salix polaris*) and the mountain dryas (*Dryas octopetala*). Thus we may be confident that the lemmings discovered in Pleistocene times in England, France, Belgium and a large part of Germany are proof of climatic conditions similar to those of the present circumpolar region. We must conclude that the borders of the ice caps were surrounded by tundra or barren ground conditions at several Pleistocene stages. The lemmings probably dwelt in the immediate neighborhood of the glaciers. The existing tundras are characterized by frozen subsoil and the absence of trees or shrubs except along the river borders.

The reason for associating the woolly mammoth with this fauna is that the mammoth as depicted by the men of the Postglacial Stage agrees precisely in its form, its proportions, and its hairy covering with the mammoths which have been discovered in the frozen subsoil of northern Siberia and are washing out in large numbers along the northern Siberian and American coast at Eschholtz Bay and elsewhere. At Thiede near Braunschweig, a classic locality, the lemming remains are associated with those of the arctic fox, arctic hare, reindeer, musk-ox and mammoth. Thus the comparison of certain regions of Pleistocene France and Germany with arctic Eurasia and the barren grounds of northern Asia and North America is based on the strongest evidence.

MIGRATION THEORY OF FLORAS AND FAUNAS

The principal contributors to the theory of northward and southward migrations and to the succession of faunas and floras are Nehring (1880-1896), Woldrich (1882-1896) and Penck (1896-1909). Such alternation is held by Penck to be demonstrated in Switzerland, where during the Third or Riss glaciation the woolly mammoth and woolly rhinoceros

RECENT PREHISTORIC	of	III PURE FOREST MEADOW FAUNA	Present
POSTGLACIAL (Severe climate)	wes to t Fau	II "REINDEER PERIOD," TUNDRA, STEPPE, ALPINE AND MEADOW FAUNA	Cold Climate
IV GLACIAL			
(Steppe climate)			
3rd INTERGLACIAL	pe		Temperate climate excepting near the glaciers
III GLACIAL	pl el G C		
2nd INTERGLACIAL	pe	I MINGLED AFRICAN- ASIATIC AND	
		FOREST-MEADOW FAUNAS	
II GLACIAL	pl ne		
1st INTERGLACIAL	p		
I GLACIAL	in		
GEOLOGIC AND CLIMATIC STAGES	to re P C	FAUNAS HABITATS	
<p>Diagram illustrating the areas covered all except the areas close to the ice. The steppe forms covered Europe.</p>			

²¹ *Hyæna spelæa* and *Felis leo spelæa*,

first appear in Europe, only to be succeeded in the Third Interglacial or Riss-Würm Stage by the reappearance of the warm African-Asiatic fauna, including the straight-tusked elephant (*E. antiquus*) and the broad-nosed rhinoceros (*D. merckii*). Theoretically this warm fauna was again driven out during the Fourth or Würm glaciation by the reappearance of the woolly elephant and the woolly rhinoceros. Penck³⁰ observes, as noted above, that we cannot hope to trace a continuous evolution of forms during the Pleistocene because we are not dealing with the development of one successive series in one locality but with the cyclical evolution of a number of different faunas compelled to migrate because of alternations of temperature and of flora, the mammals disappearing and returning at intervals too brief to allow of any marked evolutionary changes. Herein lies our difficulty when we attempt to distinguish between the Tundra Fauna of the Third and Fourth glaciations and the Forest Fauna of the corresponding interglacial stages, because the faunas return not only with the same generic but with the same specific types, as is especially illustrated in the case of the mammoth (*E. primigenius*) and the giant deer (*Megaceros*).

Resident Theory.—Another theory is presented in the accompanying table, namely, that during the First, Second and Third Glacial Stages the climatic conditions of Europe were temperate except in the immediate regions surrounding the glaciers. It was these glacial border regions which attracted the tundra fauna of the north, the reindeer and the woolly mammoth. Supporting this theory is the fact that the tundra and steppe fossils are found only in proximity to the ice caps and glaciated regions. It is not until the Fourth Glacial Stage and the Postglacial that the general climate of Europe was so severe as to cause the gradual emigration and extinction of the African-Asiatic fauna. At this stage remains of the tundra and steppe mammals occur in all parts of Europe, including the Pyrenees and Cantabrian Alps, but only partly extending into Spain.

Latitude and Altitude.—In considering the distribution and migration of the mammals throughout the Glacial Epoch, we must constantly keep in mind the differences of latitude and of climate which prevailed then as now between Italy, Spain, southern and northern France, Germany and Belgium; also the differences of altitude as between the lowlands of the rivers Rhone and Dordogne and the highlands of the Alps and other mountains. Italy had a more moderate climate than central Europe: the reindeer seems never to have found its way there, yet a lowering of tem-

³⁰ PENCK, A.: "Die alpinen Eiszeitbildungen und der prähistorische Mensch." Arch. Anthropol., N. S., Vol. I, No. 8, pp. 78-90. 1904.

TABLE IV.—Distribution of Forest Meadow Mammals

RECENT PREHISTORIC	Return of Alpine Fauna to the Mountains. Wide dispersal of Forest and Meadow Fauna over entire Northern Hemisphere			III PURE FOREST MEADOW FAUNA	Present
POSTGLACIAL (Severe climate)	Retreat of Tundra and Steppe Fauna. Wide southward dispersal of Tundra, Steppe and Alpine Fauna to the Pyrenees, Alps, northern Spain and Italy. Arrival of Asiatic Steppe Fauna.	hward and in Europe of Tundra	Cervus elaphus " capreolus Megaceros euryceros Ursus arctos Bison priscus Bos primigenius	II "REINDEER PERIOD," TUNDRA, STEPPE, ALPINE AND MEADOW FAUNA	Cold Climate
IV GLACIAL (Steppe climate)					
3rd INTERGLACIAL	Return of Warm and Temperate Fauna	Extinction or southward retreat of African-Asiatic Fauna	Alces machlis Equus caballus typicus Felis catus	I MINGLED AFRICAN-ASIATIC AND FOREST-MEADOW FAUNAS	Temperate climate excepting near the glaciers
III GLACIAL	3rd Tundra (<i>Rangifer</i> = <i>E. primigenius</i>) fauna in northern Germany and France, Glaciers of Alps and Pyrenees, Canstatt	<i>Hyæna crocuta spelæa</i> ³¹ <i>Felis leo spelæa</i> ³¹ <i>Dicerorhinus merckii</i> ³¹ <i>Elephas antiquus</i> <i>Elephas trogontherii</i> ³¹ <i>Hippopotamus major</i> ³¹ <i>Canis aureus</i> <i>Macacus</i> <i>Felis pardus</i> <i>Dicerorhinus etruscus</i> ³¹ <i>Machærodus latidens</i> ³¹ <i>Equus stenonis</i> <i>Hyæna striata</i> <i>Elephas meridionalis</i> ³¹	" <i>lynx</i> <i>Vulpes alopex</i> <i>Ursus spelæus</i> <i>Felis catus</i> <i>Sciurus vulgaris</i> <i>Canis lupus</i> <i>Sus scrofa</i> <i>Meles taxus</i> <i>Alces latifrons</i> <i>Castor fiber</i> <i>Trogontherium cuvieri</i> <i>Lutra vulgaris</i> <i>Gulo luscus</i> <i>Equus mosbachensis</i> <i>Ursus deningeri</i> <i>Ursus arvernensis</i> <i>Cervus sedgwicki</i> <i>Cervus carnutorum</i>		
2nd INTERGLACIAL	Return of Warm and Temperate Fauna				
II GLACIAL	2nd Tundra (<i>Rangifer</i> = <i>E. primigenius</i>) fauna in N. Germany, Mauer, Steinheim, etc.				
1st INTERGLACIAL	Return of Warm and Temperate Fauna				
I GLACIAL	1st Tundra (<i>Ovibos</i>) fauna in Great Britain	Survival of Pliocene and fresh invasions of African-Asiatic Fauna			
GEOLOGIC AND CLIMATIC STAGES	Early TUNDRA migrations into northern Europe and cold regions of Britain, Alps and Pyrenees	"WARM" AFRICAN-ASIATIC FAUNA, frequenting or migrating into Temperate and Sheltered Regions, remote from the Ice Caps	EURASIATIC FOREST AND MEADOW FAUNA, frequenting Cool temperate meadows and forests. Regions bordering and remote from the Ice Caps	FAUNAS	
	CIRCUMGLACIAL HABITATS AND GLACIAL MIGRANTS	TEMPERATE NON-GLACIATED HABITATS AND INTERGLACIAL MIGRANTS		HABITATS	

Diagram illustrating the author's theory that until the Fourth Glaciation the African-Asiatic-Eurasiatic Forest Meadow Mammals covered all except the areas close to the ice. The tundra forms were confined to the ice borders until the Fourth Glaciation, when the tundra and steppe forms covered Europe.

³¹ *Hyæna spelæa* and *Felis leo spelæa*, the sole survivors of the African Asiatic Fauna in the Cold Reindeer period of IV Glacial and Postglacial times.

perature in Italy is indicated by the fact that the Alpine mammals such as the marmot (*Arctomys marmotta*), chamois (*Rupicapra*) and steinbok (*Ibex*) came down to the plains.³² The "old elephant" (*E. antiquus*) fauna appeared in Italy earlier than in northern Europe. Similarly the hippopotamus survived in Italy longer than in France and Germany, so it is not surprising to find its remains associated with those of the broad-nosed rhinoceros (*D. merckii*) in a cave near Mentone on the French Riviera which belongs just prior to the Postglacial period of Aurignacian culture corresponding with the period immediately succeeding the Fourth glaciation.³³ Italy was a forested country at the time that central Europe was tundra-like or steppe-like.

Culture Stages.—Under all these varying conditions of climate human evolution progressively advances, and where the "species" of lower mammals fail us the successive human culture stages enable us to sharply distinguish the intervals of time.

Repetition of Loess Depositions.—According to Wüst³⁴ (p. 229) the First (I) and Second (II) Glacial and the First Interglacial Stages (1st) are represented in the single northern (Saxonian + Scanian) glaciation of Thuringia. The successive depositions of loess therefore occurred as follows:

Postglacial Stage, the youngest loess. Postglacial terraces.

IV (WÜRM) GLACIAL STAGE, equivalent to northern glaciation III.

3rd (*Riss-Würm*) Interglacial Stage, younger loess. The lower terraces of the 2nd (*i. e.*, 3rd Interglacial).

III (RISS) GLACIAL STAGE, equivalent to glaciation II of the north.

2nd (*Mindel-Riss*) Interglacial Stage, older loess. The higher and middle terraces of the First (*i. e.*, 2nd) Interglacial.

I-II (GÜNZ-MINDEL) GLACIATION, equivalent to glaciation I of Thuringia.

FIRST GLACIAL STAGE—GÜNZ, SCANIAN, NEBRASKAN

The First Glacial Stage is believed to have been nearly contemporaneous in Europe and North America. It is estimated (Penck) that the various ice caps reached the climax of their advance 520,000 years ago and that the snow line in the Alpine Region descended 1,200m. lower than the present snow line. In the north of Germany and in Sweden

³² ISSEL, A.: "Liguria geologie e preistorica." Ref. by Boule in *L'Anthrol.*, pp. 602-604. 1893.

³³ PENCK, A.: "Die alpinen Eiszeitbildungen der prähistorische Mensch." *Arch. Anthropol.*, N. S., Vol. I, No. 8, pp. 78-90. 1904.

³⁴ WÜST, EWALD: "Die pliozänen Ablagerungen des Travertingebietes der Gegend von Weimar und ihre Fossilienbestände in ihrer Bedeutung für die Beurteilung der Klimaschwankungen des Eiszeitalters." *Zeitschr. f. Naturwissensch.*, Band 82, Heft 3-5, pp. 161-252. Leipzig, 1910. Published Mar., 1911.

the deposits of this glacial advance are known as the old "Diluvium" or the "Oldest Drift;" the advance is termed the *Scanian* by Geikie. In the Alpine Region it has been termed the *Günz* by Penck and Brückner, and the drift deposits have a general thickness of 30m. At about the same time a great ice cap was formed in British North America west of Hudson Bay from a centre known as Keewatin which sent its ice sheets into Iowa and Nebraska. The resulting Nebraskan deposits, consisting largely of compact boulder clays, are often thickly set with woody ma-



FIG. 8.—Chief centers of North American glaciation
Keewatin, Labradorean, Cordilleran. After Leverett.

terial gathered from forests of spruce and other coniferous species that indicate the development of a cool temperate flora in advance of the glaciation.³⁵

It does not appear that a glacial cap of any considerable extent was formed in Great Britain; but Geikie³⁶ shows that along the British coast

³⁵ The above correlation is presented chiefly on the authority of Penck and Leverett (*op. cit.*, 1910).

³⁶ GEIKIE, JAMES: *The Great Ice Age*. 2nd Ed. London, 1877.

in Upper Pliocene times cold conditions began to manifest themselves in the Pliocene Red Crag and continued with increasing intensity during the deposition of the post-Pliocene Chillesford and Weybourn Crag, which mark a culminating time in which the sea abounded in Arctic molluscs, and this may represent the first glacial stage in Britain.



FIG. 9.—Principal mammal deposits and culture stations of the Pleistocene of Europe

1. Forest Bed of Cromer (Norfolk). Sables de 2. St. Prest near Chartres (Eure-et-Loire). 3. Malbattu (Puy-de-Dôme). 4. Peyrolles (Bouches-du-Rhône). 5. Solhilac near Puy. Clay deposits of 6. Durfort (Gard). 7. Cajarc (Lot-et-Garonne). 8. Val d'Arno (Tuscany). 9. Lefte near Bergamo (Lombardy). 10. Rixdorf near Potsdam (Brandenburg). Gravels of 11. Süssenborn near Weimar. Sands of 12. Mosbach in northern Baden. Fresh-water deposits of 13. Clacton (Essex). Sands of Mauer near 14. Heidelberg (western Germany). 15. Chelles on the Marne, near Paris. 16. St. Acheul (Somme). 17. Ilford and Grays Thurrock (Essex). Lignites of 18. Dürnten and of Utznach, near Zürich. 19. Taubach near Weimar. 20. Wildkirchli cave on Mont Säntis (eastern Switzerland). Tuffs of 21. the Tiber Valley, near Rome. Caves of 22. Neandertal, near Düsseldorf (western Germany), 23. Spy, near Amur (Belgium), 23a. Krapina (Croatia), 24. Chapelle-aux-Saints (Corrèze). Caves and alluvial deposits of 25. Ternifine (or Palikao) near Oran (Algeria), 26. Pointe Pescade, near Algiers (Algeria). 27. Prince's Cave (Monaco). Sandy clays of 28. Vöklinshofen (Alsace). 29. Saalfeld (Saxe-Meiningen). Travertines, etc., of 30. Gera, Jena (Saxe-Weimar). 31. Leipzig (Saxony). 32. Solutré, north of Lyons. Loess of 33. Würzburg (Bavaria). 34. Thiede near Braunschweig (Prussia). Cave of 35. Montmaurin (Haute-Garonne). 36. Châteauneuf-sur-Charente (Charente). Caves of 37. Schweizersbild near Schaffhausen, and Kesslerloch near Thayngen (northern Switzerland). Remains of lake dwellings at 38. Wauwyl (Lucerne), 39. Robenhausen, south of Lake Pfäffikon, 40. Concise on Lake Neuchâtel (Switzerland). Peatbogs of 41. Hassleben, near Weimar. Travertines of 42. Langensalza (Erfurt) in central Germany. Caves of the 43. Island of Malta, 44. Island of Crete, 45. Island of Cyprus.

FIRST INTERGLACIAL STAGE—NORFOLKIAN, AFTONIAN, GÜNZ-MINDEL

Immediately after the deposition of the Weybourn Crag in Essex there is evidence of a climatic reaction because the overlying deposits, both estuarine and fluviatile, of the so-called Forest Bed of Cromer (Norfolk) contain a flora and mammalian fauna of warm temperate type which contrast strongly with the assemblage of the northern and Arctic molluscs in the subjacent deposits of the Red, Chillesford and Weybourn Crag. From this classic locality of Norfolk the First Interglacial Stage has derived its designation *Norfolkian*. It is also known as the *Cromerian*.

The first cold period or glacial advance was succeeded both in Europe and America by climatic conditions milder than the present. In the Alpine region Penck and Brückner have found evidences of a long Günz-Mindel interval of time, estimated relatively at 100,000 years, which separates the climax of the first or Günz glaciation from the second or Mindel, but they believe that this First Interglacial Stage was much shorter than the Second Interglacial. Owing to the warmth of the climate the snow line of the Alps is believed to have risen 300m. higher than at the present time. The deposits of this stage include the *Paludinenbank* of northern Germany; these fresh-water deposits near Berlin are of true interglacial time, since they lie between the deposits of two Glacial advances. The most abundant species, *Paludina alluviana*, has its present habitat far to the south on the borders of the Black Sea. In general the other fresh-water and land molluscs belong to modern species common to the same region to-day, indicating that climatic conditions were not greatly dissimilar from the present. The plant remains include the mosses and conifers, also indicating a climate similar to the present, but they probably do not afford evidence of the higher ranges of temperature which may have occurred at other times and places during this First Interglacial Period. In America the deposits of this First Interglacial Stage, known as the *Aftonian*, are widely distributed and yield a rich mammalian as well as a land molluscan fauna and abundant plant remains which generally indicate a temperate to warm climate.

HUMID FOREST CONDITIONS

A striking characteristic of this interglacial stage is the evidence of prolonged humid conditions of climate and abundant forestation favorable to forest-living mammals. There is no evidence either in the north of Germany or in the northern United States of loess deposits such as occur during the Second and Third Interglacial Stages and are believed to be due to recurrent arid conditions and dust storms.

FLORA OF THE FIRST INTERGLACIAL PERIOD

In the "Forest Bed of Cromer" on the eastern coast of England the arrival of *Abies* is significant because although known in Miocene times in the Arctic region of Grinnell Land this is the first appearance of the fir tree in central Europe; the fir is also found in the interglacial lignites of Switzerland and has since constituted an important member of the European forests. Including the fir, all the trees composing the forests in the region of Norfolk belong to living species, such as the maple, elm, birch, willow, alder, oak, beech, pine, spruce, still indigenous to this region, latitude $52^{\circ} 40' N$. A notable fact in examining this flora of the Norfolk and Suffolk coasts of England is its correspondence with the modern flora in spite of the immense period of time that has elapsed and the great changes in climate during which all these plants were driven to the south and again permitted to return. "However," continues Reid,³⁷ "though very similar, we find in the fossil flora several exotic species which give it a slightly different character and we notice also the absence of several modern forms." From this tree flora Reid concludes that the climate of southeastern England was nearly the same as at present, but slightly warmer.

The flora of Durfort (Gard) in southern France is associated with remains of the southern elephant (*E. meridionalis*), the etruscan rhinoceros (*D. etruscus*) and the Pliocene horse (*Equus stenonis*).³⁸ It includes numerous plants of species now represented in the Caucasus, Persia, southern Italy, Portugal and Japan. Again, in the interglacial forests of Moret (Seine valley) we find the fig (*Ficus*) and the Judas tree (*Cercis*), indicating a mild temperature. The tree flora of France like that of Norfolk thus indicates somewhat warmer conditions of temperature than prevail at the present time, a temperature of 4° of latitude to the south.

MAMMALS OF THE FIRST INTERGLACIAL STAGE

For our knowledge of the mammalian life of the Forest Bed of Norfolk and contemporaneous deposits of France we are indebted principally to Dawkins (1880, 1883), Newton (1880), Gaudry (1893), Boule (1902), and Pohlig (1907). Dawkins many years ago (1883, p. 579) estimated the ratio of living, extinct and newly arriving mammals in the Forest Bed as follows:

³⁷ REID, C., and REID, E. M.: "The Pre-Glacial Flora of Britain," Jour. Linn. Soc., Botany, Vol. xxxviii, pp. 206-227. Jan., 1908.

³⁸ GAUDRY, A.: L'éléphant de Durfort. Paris, 1893.

Survivals from the Pliocene.....	11	species
Newcomers, forms now extinct.....	6	"
Newcomers, forms still living.....	21	"

The specific determinations of many of these animals are based upon very incomplete materials and await careful revision; and upon this closer study will depend also the correlations between the various First Interglacial faunæ of Great Britain and the continent. From our present knowledge the following faunistic correlation may be made:

- Northern Life. Forest Bed of Cromer, Norfolk, England (Fig. 9, 1), typical of the northern life.
 Sables de St. Prest (Eure-et-Loire), France, (2) typical of the central life of France.
 Malbattu (Puy-de-Dôme), France, (3) typical of the central life of France.
- Southern Life. Peyrolles (Bouches-du-Rhône), France, (4) typical of the southern life of France.
 Solilhac, near Puy, southern France, (5) typical of the southern life.
 Durfort (Gard), southern France, (6) typical of the southern life.
 Cajarc, Lot-et-Garonne, (7) typical of the southern life.
 Val d'Arno (upper, or Pleistocene deposits), northern Italy, (8) typical of the southern life of Europe.

Extinctions.—The survival of a number of Pliocene mammals into this period has led certain palæontologists, such as Boule, to place the First Interglacial fauna and the Glacial stage which preceded it in the Pliocene rather than in the Pleistocene Epoch. The true Upper Pliocene fauna, however, is characterized by a number of distinctively Pliocene mammals, especially the primates, mastodons, antelopes, gazelles and tapirs. None of these animals have been found in the Pleistocene of Europe; all had become extinct.

Survivals.—This First Interglacial fauna does include, however, a number of survivals from the Pliocene, such as the sabre-tooth cats (*Machærodus*), the polycladine deer (*C. sedgwicki*), the more primitive dicerorhine rhinoceros with brachyodont teeth (*D. etruscus*), the primitive Upper Pliocene horse (*Equus stenonis*), the southern elephants (*E. meridionalis*), the hippopotami, the roedeer (*Capreolus capreolus*), the giant beaver (*Trogotherium*), the Auvergne bear (*Ursus arvernensis*), the wild cattle (*Leptobos*).

It is noteworthy that Pohlig considers the *E. meridionalis* of this stage to be of more recent type than the true Pliocene type of Italy described by Nesti; hence he terms it *E. (meridionalis) trogontherii*. It is also

noteworthy that the polycladine deer (*Cervus sedgwicki*) do not reappear in any of the subsequent Pleistocene formations of Europe.

Arrivals.—Among the new arrivals in the Forest Bed of Norfolk are the earliest members of the giant deer race (*Megaceros*) which continues into Middle Pleistocene times in Europe. We also note in the Forest Bed the presence of a form (*Caprovis*) intermediate between the goat and the sheep, as the name indicates, and most closely resembling the moufflon of Sardinia. Among the rodents the large beaver *Trogonthe-*



FIG. 10.—Giant deer, *Megaceros*, of the British Pleistocene

From a skeleton found in the Irish peat bogs. After original by Charles R. Knight in the American Museum of Natural History.

rium cuvieri succeeds the smaller ancestral species (*T. minus*) first observed in the Pliocene of the Red Crag. The giant hippopotamus (*H. major*) is certainly recorded in this region of Great Britain as well as to the south in Italy.

Among the proofs of a northerly climate is the first occurrence of the musk-ox (*Ovibus*), which is attributed by Dawkins³⁹ to the Forest Bed deposits.

³⁹ DAWKINS, W. BOYD: "On the Alleged Existence of *Ovibus moschatus* in the Forest-bed, and on its Range in Space and Time." Quart. Jour. Geol. Soc. London, Vol. 39, pp. 576-579. 1883.

Among the animals attributed by Dawkins to the Forest Bed fauna which Newton⁴⁰ considers of doubtful reference are the hyæna, the true cattle (*Bos primigenius*), the red deer (*Cervus elaphus*), the moose (*Alces latifrons*) and the giant deer (*Megaceros*). These animals are, however, certainly recorded in France (Cajarc) with the exception of the moose (*Alces*).

The presence of deer (Cervidæ) in great numbers and representing many different phyla is one of the most distinctive features of First Interglacial times. There existed numerous and varied forms of deer life both in Great Britain and southern and western Europe, attesting the presence of forests. They belong to several, probably to as many as five distinct phyla. Among these the polycladine, or "many-branched" deer so distinctive of the Upper Pliocene of the Val d'Arno now make their last appearance in Europe as Sedgwick's deer (*C. sedgwicki*) of the Forest Bed, with remarkably complex antlers closer to the *C. dicranus* of the Val d'Arno. A second Pliocene European phylum is that of the roe-deer (*C. capreolus*). A third phylum, numerous and highly diversified, is that of the giant deer (*Megaceros*) which is represented by a variety of species (*M. verticornis*, *M. fitchii*, *M. dawkinsi*). There is some doubt whether the true "deer of the Carnutes" (*C. carnutorum*) occurs here. As above noted Newton is uncertain whether the stag (*C. elaphus*) has been truly recorded in the Forest Bed. Neither the true fallow deer (*Cervus dama*) nor the reindeer (*Rangifer tarandus*) has been recorded there.

This Forest Bed fauna as a whole is an outlier of the Asiatic-African group with a strong northerly Eurasiatic forest element intermingled. We observe that browsing, forest-living and fluviatile types predominate. Among the forest-frequenting carnivores are the wolverine (*Gulo*), the otter (*Lutra*), two kinds of bear (*Ursus*), the wolf (*Canis*), the fox (*Vulpes*), the marten (*Mustela*) and a true feline (*Felis*) in addition to numerous representatives of the sabre-tooth tigers (*Machærodus*). All the above are true Eurasiatic forest types from north-temperate latitudes. Among the forest-living browsers also is a large boar related to *Sus scrofa*, the primitive browsing rhinoceros (*Dicerorhinus etruscus*) with short-crowned teeth, while in the rivers disported the giant hippopotamus (*H. major*). Among the grazing and meadow-living forms *Bos* or *Leptobos* is represented in the Forest Bed. There are also two species of horses including a lighter form resembling the *E. stenonis*

⁴⁰ NEWTON, E. T.: "Notes on the Vertebrata of the Pre-Glacial Forest Bed Series of the East of England." Geol. Mag., Vol. vii, Pt. I, Carnivora, pp. 152-155, Pt. II, Carnivora, pp. 424-427, Pt. III, Ungulata, pp. 447-452, Pl. xv. 1880.

cocchi of the Val d'Arno, and a heavier type of horse, probably forest-living.

Cool estuarine conditions are represented by the presence of the walrus (*Trichecodon*), the seal (*Phoca*) and the cormorant (*Phalacrocorax*).

The chief members of the mammalian assemblage of the First Inter-glacial Stage in Britain and France are as follows:

Southern elephants

E. meridionalis (*trogontherii*)

Dicerorhine rhinoceroses

D. etruscus

Primitive horses

E. stenonis, *E. caballus fossilis* ?

Hippopotami

H. major

Polycladine deer

C. sedgwicki

Roe deer

C. capreolus

Giant deer, *Megaceros*

M. dawkinsi, *M. verticornis*

Primitive cattle

Bos primigenius

Giant beaver

Trogontherium cuvieri

Sabre tooth cats

Machærodus ? *cultridens*

Wolverines or gluttons (in Great Britain)

Gulo luscus

Bear of the *Ursus arctos* type

Otters and martens

Wolves and foxes

Walrus (in Great Britain)

Trichecodon huæleyi

(In Italy only)

Straight-tusked mammoths

E. antiquus

(In France)

Bison

Bison ? *priscus*

Stag

Cervus elaphus

mus (*H. major*), the giant beaver (*Trogontherium*). In France occur the first remains attributed to the bison (*B. priscus*). In Durfort was

FIRST INTERGLACIAL OF FRANCE

The Lower Pleistocene deposits of France, which are approximately of the same age as the Forest Bed (Norfolk), are those of St. Prest (near Chartres), of Durfort (Gard), of Solilhac (near Puy) and the recently discovered phosphorite deposits of Cajarc (Lot-et-Garonne) (Fig. 9, 7). All these beds are considered by Boule as of Upper Pliocene age; they are placed in the transition period between Pliocene and Pleistocene times by Harlé and Stehlin⁴¹ as well as by Depéret (St. Prestien).

We are disposed to consider all these deposits of approximately the same age as the Forest Bed, namely, Early Pleistocene. In none of them have remains of primates, mastodons, tapirs or other characteristic Upper Pliocene mammals been found. On the other hand, these beds contain several forms surviving from the Pliocene, such as the southern mammoth (*E. meridionalis*), the etruscan rhinoceros (*D. etruscus*), a primitive species of horse (*E. stenonis*), the giant hippopotamus

⁴¹ HARLÉ, E., and STEHLIN, H. G.: "Une Nouvelle Faune de Mammifères des Phosphorites du Quercy." [Cajarc.] Bull. Soc. Géol. France, Ser. 4, Vol. IX, pp. 39-52. 1909.

obtained the skeleton of the southern mammoth described by Gaudry.⁴² The giant deer (*Megaceros*) are represented at St. Prest by the species *C. carnutorum*, or "deer of the Carnutes."

The most recently discovered fauna of this age is that of Cajarc in the northern part of the Rhone basin. Harlé and Stehlin consider the Cajarc fauna as transitional between that of St. Prest and Durfort and that of Montmaurin which we attribute to Second Interglacial times. The mammoth (*E. meridionalis*) is of a more recent type than the Upper Pliocene form of Italy. The bison is a very large animal. Especially important is the fact that these authors positively identify here remains of deer which are related to the stag or red deer of Europe (*Cervus elaphus*), leaving the species doubtful. There is also at Cajarc a large badger (*Meles taxus*) which is characteristic of early Pleistocene times, and a small wolf (*Canis*) no larger than the jackal. There is also a small species of sabre-tooth tiger (*Machærodus*).

Southern Elephant (*Elephas meridionalis*).—The "southern elephant" is Faulkner's "pre-Glacial variety of the mammoth." It belongs to the same general group as the other mammoths (*E. trogontherii*, *E. primigenius*) and the Columbian mammoth (*E. columbi*) of America. The southern elephant of First Interglacial times

belongs to a somewhat more advanced type than that of the Upper Pliocene of the Val d'Arno; the Forest Bed specimens are, in fact, attributed by Pohlig⁴³ to his species *E. trogontherii*. This mammoth series is distinguished both from the African (*Loxodonta*) and the Indian (*Elephas*) elephants by the peculiarly flattened and concave forehead and the high, peaked cranium. It is probably descended from *E. planifrons* of the Pliocene and in tooth and skull structure it resembles the *E. hysu-*

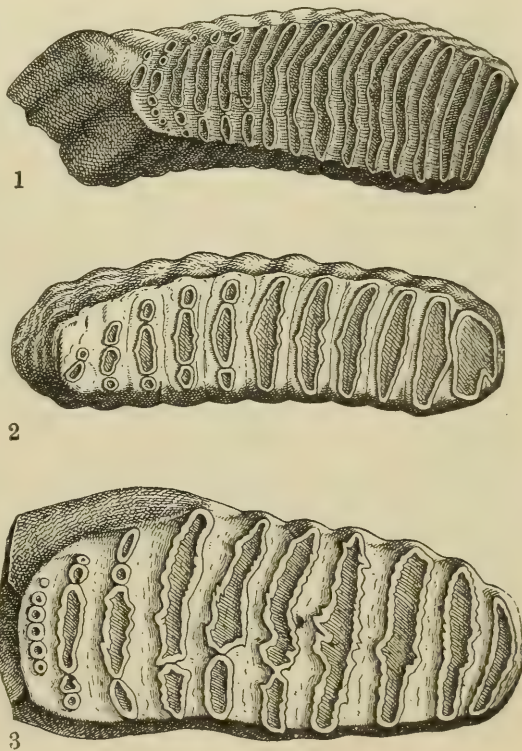


FIG. 11.—Molars of Pleistocene elephants

- (1) *Elephas primigenius*,
- (2) *Elephas antiquus*,
- (3) *Elephas meridionalis*.

After Lartet.

⁴² GAUDRY, A.: L'Éléphant de Durfort. Paris, 1883.

⁴³ POHLIG, H.: "Über *Elephas trogontherii* in England." Monatsber. Deutsch. Geol. Ges., Vol. 61, No. 5, pp. 242-249. 1909.

Arctos of the Upper Pliocene Siwaliks of India. Thus two distinct stages of the southern mammoth are known, the more primitive, occurring at the close of the Tertiary in the Pliocene of the Val d'Arno, distinguished by very low, broad grinding teeth with thick enamel, the other more progressive stage, occurring in the Forest Bed, at Durfort, and in the Pleistocene deposits of the Val d'Arno, and distinguished by dental plates of thinner enamel. The latter is said to be the original type of Nesti, who founded the species, but the matter of specific type requires investigation.

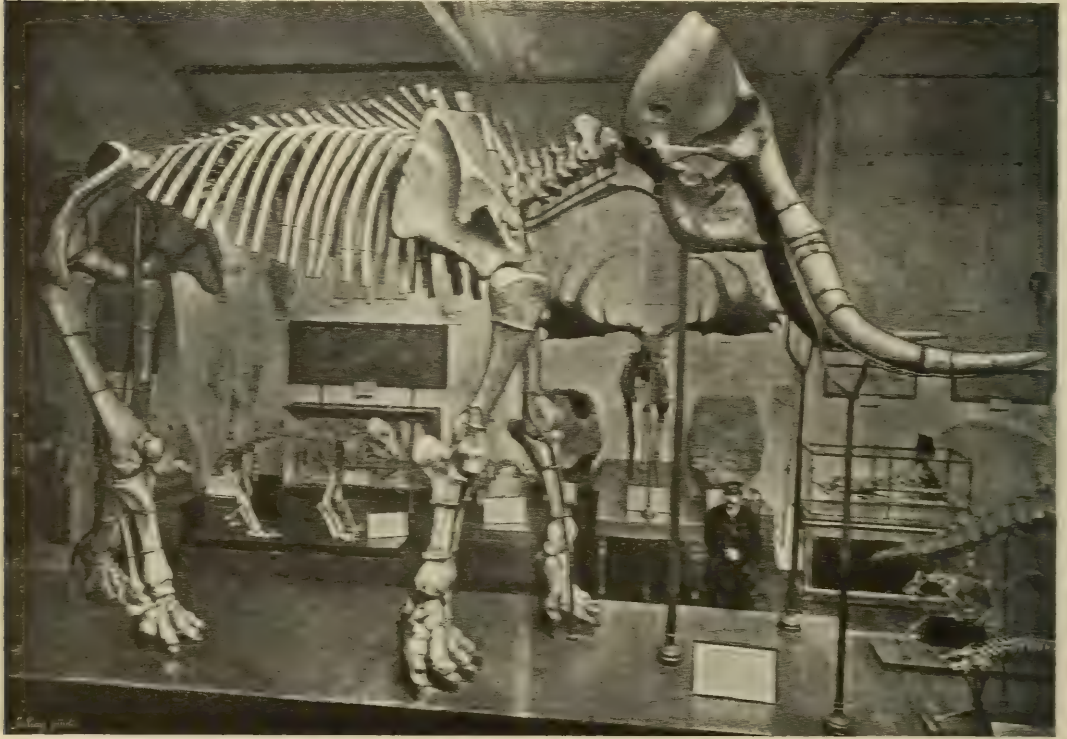


FIG. 12.—*Skeleton of Elephas meridionalis of Durfort*

Gallery of Palaeontology in the Museum d'Histoire Naturelle, Jardin des Plantes, Paris.
After Gaudry.

The southern elephant is best known from the magnificent specimen found at Durfort and mounted under the direction of Gaudry in the Paris Museum. The height at the shoulders is 3.83 m., or 12 ft., 9-1/5 in. This animal was much taller than the true mammoth (*E. primigenius*) which first appears chiefly in the Third Glacial Stage. The tusks were shorter and less bent. We may infer from its original warm-temperate habitat that it was partially hairy but not covered with wool like *E. primigenius*.

The following table of comparison of the relative heights of the great Pleistocene and recent elephants is based so far as the extinct forms are concerned on a series of approximations because it is very difficult to

estimate the height of these animals from the skeleton. In almost all cases of mounting these animals in museums the tips of the dorsal spines are unduly elevated above the superior spine of the scapula, which gives an exaggerated estimate of the height.

	General estimated height at shoulder	
	English measure	Meters
<i>E. imperator</i> , the imperial mammoth of North America, lower Pleistocene.....	13' 6"—14'	4.2672
The straight-tusked elephant, <i>E. antiquus</i> of Europe. (?) estimated (Pohlig, Pilgrim) at.....	15'—16'	4.8768
The southern elephant of Europe, <i>E. meridionalis</i>	12' 9"	3.8862
The largest living African elephant, <i>L. africanus</i>	11' 3"—11' 4"	3.4544
The Columbian mammoth of North America, <i>E. columbi</i> .	9'—11'	3.3528
The Indian elephant of Asia, <i>E. indicus</i>	9' 10"—10'	3.048
The true, or northern mammoth, <i>E. primigenius</i> (teste Lucas)	9' 6"—10' 6"	3.2004
The living pigmy elephant of the Congo, <i>L. cyclotis pumilio</i> (teste Hornaday).....	4' 5"	1.3462
The dwarfed elephant of Crete (<i>E. antiquus creticus</i>), Malta (<i>E. antiquus melitensis</i>) and Cyprus.....	5'	1.524
The American mastodon, <i>Mastodon americanus</i>	9' 6"	2.8956

Hippopotami.—The hippopotamus is the invariable companion of the southern elephant and later of the *Elephas trogontherii*; it survived even in northern Europe until the middle of the Third Interglacial Stage. Outside of Asia the oldest hippopotamus remains known are from the Lower Pliocene of Gravittelli in Sicily;⁴⁴ it is compared by Seguenza (1902) with the *H. sivalensis* of India but is clearly distinct from this species. The *H. hipponensis* of Gaudry is confined to the Middle Pliocene of North Africa and throws no light on the phylogeny of the hippopotami. These animals appear in the Lower Pliocene of India and of Sicily and in the closing Pliocene of Italy, India, and North Africa and perhaps China; in the Quaternary they spread into Java, India, Madagascar, Africa from north to south, the Mediterranean Islands, and from Spain and Italy on the south to England and west Germany on the north. Until additional data are secured it is difficult to decide whether this family originated in Africa (Stehlin, 1899) or in Asia (Schlosser, 1903).

Sabre Teeth.—Stromer⁴⁵ has recently traced the history of the machærodonts in north Africa, Asia and Europe. A form closely similar to

⁴⁴ STROMER, ERNST: "Mitteilungen über Wirbeltierreste aus dem Mittelplicän des Natrontales (Ägypten). 3. Artiodactyla: Bunodontia: Flusspferd." Zeits. d. Deutsch. Geolog. Ges., Band 66, Abhandl., Heft 1, pp. 1-33. 1914.

⁴⁵ STROMER, ERNST: "Mitteilungen über Wirbeltierreste aus dem Mittelplicän des Natrontales (Ägypten)." Zeitschr. d. Deutsch. Geologisch. Gesellschaft, Band 65, Abhandl., Heft 3, pp. 350-372. 1913.

M. aphanistus Kaup is the first known member of the sub-family to be discovered in Africa. He observes that the hyænas and otters (*Lutra*), the seals (*Pristiphoca*), and sabre teeth (*Machærodus*) speak strongly for a connection between North Africa (Egypt), Asia and Pliocene Europe. The sabre-tooth survives into the First, Second, and possibly into the Third Interglacial Stage (see note on Chellean culture).

Moose (Alces).—The earliest representative of the moose⁴⁶ is the *Alces latifrons* Dawkins from the Forest Bed of Cromer. It also occurs in the sands of Mosbach and of Mauer (Second Interglacial) and in the sands underlying the lower travertine layers of Taubach (Third Interglacial), always distinguished by the relatively simple palmation of its antlers from the existing *A. machlis*. The animal is also recorded in the Third Interglacial layer of Rixdorf and it survived in Germany into post-Neolithic times.

PROBLEMATIC EVIDENCE OF MAN

Saint-Prest is the most ancient Lower Pleistocene deposit in the basin of Paris.⁴⁷ Coarse sands and gravels form part of the "high terrace" 50m. above the present level of the river Eure and contain a First Interglacial fauna of *Elephas meridionalis* and *Equus stenonis* as well as the "eoliths" known as *Reutelian*. This constitutes the Saint-Prestien stage of Depéret.

The locality of Saint-Prest is famous because in 1863 Desnoyer first reported the discovery of a number of bones with incision lines which he considered to be the work of man. These deposits were at the time regarded as Pliocene and gave rise to the theory of the occurrence of man in Pliocene times. The human origin of these incisions has long been a matter of dispute and is still doubtful. The associated fauna at Saint-Prest includes the southern elephant, the etruscan rhinoceros, the hippopotamus, the giant beaver, three species of beaver and one of the bison. There is thus little doubt that this deposit is of First Interglacial age. Supposed confirmation of Desnoyer's discovery was the alleged finding by Abbott of several worked flints, two *in situ*, in the Cromer Forest Bed.

This question has become more or less identified with the eolithic theory which postulates a long stage of the artificial use of flints antecedent to the pre-Chellean and Chellean Stages, which are here considered as belonging in the Third Glacial Stage, although some authors place the pre-Chellean in the First Interglacial Stage.

⁴⁶ DIETRICH, W. O.: "Neue fossile Cervidenreste aus Schwaben," Jahreshefte des Vereins f. vaterländische Naturkunde, Jahrg. 66, pp. 320-336. 1910.

⁴⁷ HAUG, ÉMILE: "Traité de Géologie. II. Les Périodes géologiques," p. 1807. Libr. Armand Collin, Paris, 1908-1911.

*Eolithic Theory.*⁴⁸—Following Desnoyer's discovery in 1863 was that of L'Abbé Bourgeois in 1867, who found in the Miocene of Thenay, Loire-et-Cher, flints supposed to be the work of man. In 1877 Rames brought to notice flints from the Upper Miocene volcanic ash beds of Puy-Cournay, Cantal, in central France. In 1892 Brown proposed the term "eoliths" to distinguish these supposedly primitive artifacts from the "palæoliths" of Lubbock (Fig. 13). The Belgian geologist Rutot has devoted many years to the development of the eolithic theory and has

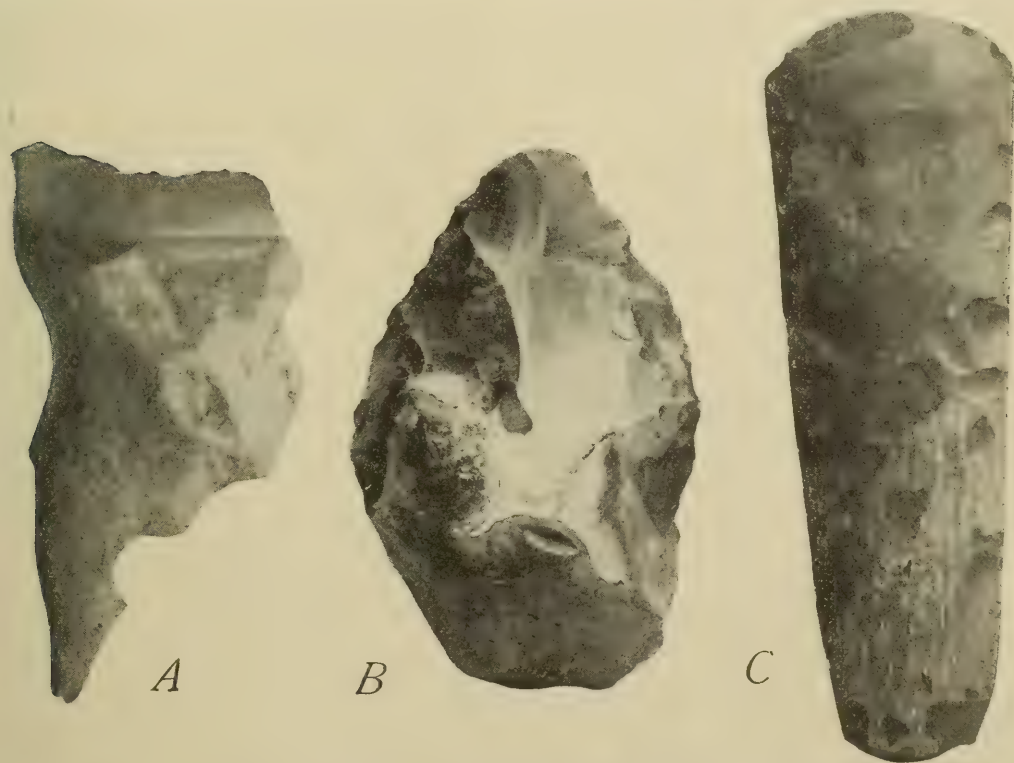


FIG. 13.—*Eolithic, Palæolithic and Neolithic implements*

A Eolith, Mafflean Epoch, Belgium. B Palæolith, Chellean Epoch, Milton Street, Kent, England. C Neolith, Upper Robenhausian Epoch, Gille Leie, Denmark. Photograph by MacCurdy, 1909.

attempted to prove that like the Palæolithic the Eolithic period is capable of subdivision into a number of stages or industries which are geologically demonstrable.

The supposed eolithic flints are very rough, but rude as they are they generally exhibit one part shaped as if to be grasped by the hand while the other part appears to be edged or pointed for cutting.⁴⁹ It is gener-

⁴⁸ MACCURDY, G. G.: "The Eolithic Problem. Evidences of a Rude Industry Antedating the Paleolithic." *Amer. Anthropol.*, N. S., Vol. VII, No. 3, pp. 425-479. July-Sept., 1905.

⁴⁹ PENCK, A.: "The Antiquity of Man." Lecture before Washington Acad. of Sci., Feb. 1, 1909. *Abstr. Science*, N. S., Vol. xxix, No. 739, pp. 359-360. Feb. 26, 1909.

ally admitted that these flints are mostly of accidental shapes and show little or no proof of being fashioned by human hands. The chief difficulty in the eolithic theory is that flints of a similar character occur in deposits of Upper Oligocene age (Rutot) and may even be found in deposits of Lower Eocene age (Breuil). The leading French archæologists, Cartailhac, Breuil, Obermaier, Boule, accordingly reject the eolithic theory entirely. Breuil considers that the various eolithic shapes are entirely accidental products due to pressure of closely compacted flints. Boule observes:⁵⁰ "As to the 'eoliths' I have combatted the theory not only because it seems to me improbable, but because a long geological experience has shown me that it is often impossible to distinguish stones split, cut or 'retouched' by purely physical agents from certain products of rudimentary workmanship."

It does not appear that the eolithic theory has been strengthened in recent years. If eoliths are to be regarded as human artifacts the antiquity of man or of a prehuman type given to shaping stone implements would be vastly increased. It is probable that the ancestors of early man possessed grasping power of the hand. The only known Miocene and Pliocene primate of Europe which might be considered as an eolith-maker or eolith-user is *Dryopithecus*; all the other known pre-Pleistocene primates belong to some one of the existing phyla of monkeys, baboons, or apes.

Pithecanthropus erectus.—Of late Pliocene or early Pleistocene age is the *Pithecanthropus erectus* of Trinil, Java, discovered by the Dutch army surgeon Eugen Dubois in the year 1891. The remains were recorded by Dubois as of Upper Pliocene age because of their association with a rich fauna containing *Stegodon ganesa*, *Elephas hysudricus*, and other mammals similar to those of the Upper Pliocene of the Siwaliks of India. Reëxamination of the Kendeng stratum in which *Pithecanthropus* occurs, by Holz (1907), Elbert (1908) and others appears to demonstrate that the *Pithecanthropus* occurs in strata corresponding with an early Pluvial period following a period of low temperature which would appear to accord with the early Pleistocene of Europe. It is therefore generally agreed that *Pithecanthropus* is of early Pleistocene age. Following the monographic description of this very important type by its discoverer Dubois⁵¹ was the keen analysis of Schwalbe,⁵² who regards

⁵⁰ BOULE, MARCELLIN: "L'Homme fossile de la Chapelle-aux-Saints." *Ann. de Palæont.* Vol. VI, pp. 111-172, pl. XVII-XX, 1911; Vol. VII, pp. 21-192, pl. IV-XIX, 1912; Vol. VIII, pp. 1-71, 1913.

⁵¹ DUBOIS, ETG.: "Pithecanthropus erectus. Eine Menschenähnliche Uebergangsform aus Java." 4to. Landesdruckerei, 39 pp., 2 pl. Batavia, Java, 1894.

⁵² SCHWALBE, G.: "Ueber fossile Primaten und ihre Bedeutung für die Vorgeschichte des Menschen." *Mitteil. Philomat. Ges. Elsass-Lothringen*, Vol. IV; No. 1, Decade 16, 1908. Strassburg, 1909.

these remains as representing either a direct or indirect ancestor of a human phylum which stands intermediate between that of the apes and Neanderthal man (*H. neanderthalensis*) both in respect to its high brain capacity and the structure of its femur. The unusually straight femur indicates an erect attitude, to which the specific name *P. erectus* applies; in fact, from the structure of the thigh bone Dubois concluded that the "Trinil Ape-Man" had free use of the arm and hand, which were now no longer required for locomotion, and that the hand was already far advanced in the line of differentiation which developed it into an organ of touch and capable of fashioning tools.

LIFE OF THE MEDITERRANEAN ISLANDS

It appears that the continental elevation of southern Europe in early Pleistocene times established migrating routes or land connections between the islands of the Mediterranean with Europe on the north and Africa on the south. Rüttimeyer (1869) was one of the first to maintain that north Africa, including Morocco, Algeria and Tunis, was stocked with mammals by way of Gibraltar and perhaps also by way of Sicily and Malta. In the islands of Malta, Cyprus and Crete as recently explored by Bate⁵³ we have proof, first, of a long period of connection with the neighboring continents through elevation, and second, of the isolation of the islands through subsidence. The isolation is followed by the dwarfing of several types of large mammals which, confined on the islands were made captive by the sea. Pohlig believes⁵⁴ that toward the end of the First Glacial Stage large mammals migrated to Sicily which at that time was connected both with Europe and Africa. The land bridges then became submerged and the large mammals dwindled in proportions through interbreeding and isolation into dwarf races. It appears probable that Cyprus became isolated as an island first, because the extinct *Elephas cypriotes* and *Hippopotamus minutus* are both more primitive than the species of Malta and Sicily. That Malta retained its connection with Sicily for a long period is indicated by the common occurrence in the cavern deposits on both islands of the two species *Elephas mnaidriensis* and *Hippopotamus pentlandi*. The dwarf elephant race (*E. melitensis*) characteristic of Malta has also been found on the mainland near Rome, which would seem to indicate that land connection between the Italian mainland and Malta was renewed more than once.

⁵³ BATE, D. M. A.: "On Elephant Remains from Crete, with Description of *Elephas creticus* sp. n.," Proc. Zoöl. Soc. London, pp. 238-250. Aug. 1, 1907.

⁵⁴ POHLIG, H.: "Eine Elefantenhöhle Siciliens und der erste Nachweis des Cranialdomes von *Elephas antiquus*," Abhand. königl. bayer. Akad. Wissensch., cl. ii, Bd. xviii, Abth. 1, pp. 75-108, pll. i-v, 1895. Sep. Munich, 1893.

The diminutive elephants of the Mediterranean islands were all descendants of the straight-tusked species *E. antiquus*. The researches of Bate confirm this relationship. They attained a height not exceeding five feet. The adaptability to which *E. antiquus* owed its wide geographic distribution and continued existence through a long period of time may account for its survival in the Mediterranean islands despite rapid diminution in size under adverse circumstances. The true African elephant (*Loxodonta*) never crossed the Mediterranean.

The reduced existing fauna of the Island of Cyprus contains a mingling of Eurasiatic and north African mammals and shows the effects of deforestation in historic times. Descendants of Eurasiatic ancestors prevail in the Mediterranean islands. The recently discovered *Myotragus balearicus* of the Pleistocene cave deposits of the Island of Majorca is now regarded as related to the Rupicaprinæ or Alpine chamois type (Andrews).

SECOND GLACIAL STAGE—SAXONIAN, MINDEL, KANSAN

The second glaciation was the greatest both in Europe and America. We observe that the most extended drift sheets are those in the Scandinavian region, on the British Isles, around the northern Swiss Alps, and from the Keewatin center west of Hudson Bay in British America. The whole rise and fall of the Mindel glaciation in the Alps is estimated by Penck as occupying a very long period of time. The snow line in the Alpine region descended 1,300m. lower than at the present time.

The only notable exceptions are in the Labrador region of eastern North America where the main ice field was formed at a later stage, known as the Illinoian. It also appears that the Third Glacial or Riss drift of the western Alps is the greatest in that region and of similar age to the Illinoian.

In this second glacial advance the Scandinavian ice field reached its farthest southerly limits. In northwestern Europe this main Saxonian (Geikie) glaciation extended to the northern slopes of the Carpathians, the Sudetes, the Erz Gebirge, the Thuringian and the Harz Mountains. From these ice sheets were given off the "Older Drift," or "Lower Diluvium" of northern Germany, and in the Swiss Alps this Second glaciation sent out its Mindel drift as the most extensive fringe along the northern borders of the Alps; on the eastern and southern borders of the Alps the Second Glaciation was about as extensive as the Third glaciation; on the western borders of the Alps the Second glaciation was less extensive than the Third. Similar conditions prevailed in America; from the Keewatin Centre the ice cap extended its drift southward into

Missouri, Iowa, Kansas and Nebraska beyond the limits both of the First and the Fourth glaciation.

Thus the Saxonian drift of North Germany, the Mindel drift of the Swiss Alps and the Kansas drift of America are correlated (Penck, Leverett) both by their great antiquity and by their very wide extent. The eminent geologist Wahnschaffe, however, correlates the "Old Drift" of the north German lowland with the Third or Riss glaciation instead of with the Second.

SECOND INTERGLACIAL STAGE—MINDEL-RISS

Penck regards the Second Interglacial or Mindel-Riss Stage as by far the longest of the interglacial intervals in the Alpine region, estimating the period between the maximum Second glaciation (Mindel) and maximum Third (Riss) as high as 360,000 years. In America also by comparing the erosion of the Second Glacial (Kansan) drifts with those of the Third Glacial (Illinoian) drifts it would appear that the Second Interglacial Yarmouth Stage was of greater duration than the entire interval between the Third Glacial and present time. In the north German lowlands it is shown to be a long interval from the amount of sedimentation effected by the interglacial rivers and streams, but whether in this region it is longer than the First Interglacial Stage is doubtful (Leverett, 1910, p. 273).

MOISTURE FOLLOWED BY ARIDITY

In course of this long warm Second Interglacial Stage the climate again moderated, becoming slightly warmer than the climate of to-day. The climate immediately following the retreat of the ice was cool and moist, then followed a long warm stage, but this stage was finally succeeded by a period of aridity both in Europe and America in which the first loess deposits occurred. In Russia also the Second Interglacial seems to begin with a cool and moist phase followed by a more arid or steppe-like climate favorable to the deposition of loess. It would appear that the height of the interglacial aridity was reached during the deposition of the loess. The "Older Loess" deposition certainly began both in Europe and America during the Second Interglacial Stage although in neither country is the "Older Loess" so continuous or so thick a deposit as the "Newer Loess." In Europe the "Old Loess" lies between the "Old Drift" of the First and Second Glacial advances and the "Middle Drift" of the Third Glacial advance. At Mauer near Heidelberg the loess lies immediately above the Upper Mauer sand layer which contains an arctic-tundra fauna (Förster, 1913). The various layers of loess are of the

utmost importance both in Europe and America in the correlation of human and mammalian life, also in their significance as to the climate of interglacial times. Loess consists of a fine, porous, silicious, calcareous silt, usually of light brown color, characterized by a peculiar competency to stand in vertical walls during erosion. Its origin and transportation are believed to have been partly sub-glacial, partly fluvial, partly æolian. The fine mud carried by the sub-glacial streams in glacial times became desiccated and redistributed by the wind. Penck (1904) describes the Pleistocene loess as formed in districts traversed periodically by great streams leaving dry mud which in arid periods was redistributed by æolian agencies. Its Pleistocene distribution is quite independent of altitude since it occurs in the interglacial deposits of Europe from sea level to a height of 1,500m.

CLIMATE

A considerable part of the elevation of the Swiss Alps apparently took place (Penck, 1910) during the Second Interglacial Stage, and this increased altitude is considered by some European authorities to be the cause of the greater extent of the Third glaciation in the western Alps.

The Höttinger breccia near Innsbruck is referred by Penck (1909, p. 1157) to the Second Interglacial Stage with its rich flora indicating a climate warmer than that of present times; this breccia lies on one of the old "High Terraces" of Second Interglacial times. The plants include the fir (*Pinus sylvestris*), spruce (*Picea* sp.), maple (*Acer pseudoplatanus*), buckthorn (*Rhamnus frangula*), several willows (*Salix nigricans*, *S. glabra*, *S. incana*, *S. triandra*), the wayfaring tree (*Viburnum lantana*), yew (*Taxus baccata*), elm (*Ulmus campestris*), strawberry (*Fragaria vesca*), self-heal (*Prunella vulgaris*), beech (*Fagus silvatica*), and mountain ash (*Sorbus aucuparia*), buckthorn (*Rhamnus Hættingensis*), related most closely to *R. latifolia*, now living in the Canary Isles, the box (*Buxus sempervirens*), also a southern species; and most important of all a rhododendron (*R. ponticum*) which now lives in the Caucasus five degrees south of the latitude of Innsbruck and in a climate on the average 3° C. warmer. Taking all the facts into consideration Penck concludes that the climate of Innsbruck in the days of the Hötting breccia was 2° C. higher than it is now. In correspondence with this the snow-line stood 1,000 ft. above its present level, and the Alps save for the higher peaks were almost completely denuded of ice and snow.⁵⁵

A picture of the flora of the Second long warm Interglacial Stage is also afforded in the Quaternary tuffs of Provence, where the remains of

⁵⁵ SOLLAS, W. J.: *Ancient Hunters and their Modern Representatives*, p. 27. 8vo. MacMillan & Co. London, 1911.

plants are associated with elephants of the *E. antiquus* stage. "The flora of the Quaternary tuffs," observes Saporta,⁵⁶ "is composed almost entirely of woody forms living in valleys and by the sides of streams." It is for the most part analogous with the present flora of Provence. Of the thirty-seven species, twenty-nine still occur in this region. Among the forms which have since retreated to the south are the sweet bay (*Laurus nobilis*) and another species of laurel (*L. canariensis*) which is now confined to the Canaries. The greater humidity of the time is indicated by the presence of species of pine which require more moisture. As in the Norfolk Interglacial, the figs (*Ficus*) and the Judas trees (*Cercis*) flourished. The ash (*Fraxinus*) is of a species now found in Corsica and Italy. On the whole, the forest trees and forest ground flora are surprisingly modern, including oaks, elms, poplars, willows, lindens, maples, sumacs, dogwood, hawthorn. Among the climbing plants are the vine (*Vitis*) and clematis (*Clematis*).

MAMMALS

This life period was first observed by Lyell and Evans in Essex, England, and was subsequently recognized in Germany and France. Geologically the deposits are partly of fluvial origin, consisting chiefly of river sands and gravels in which the remains of hippopotamus, elephants and rhinoceroses occur. These animals were formerly cited as proof of an almost tropical climate, but the evidence of the flora, enumerated above, and the equally numerous hardy types of animals tend to modify the former theories as to extremely warm Second Interglacial temperatures. The geographic connections of Europe with the south through the land bridges of Lower Pleistocene times still persisted in Italy in whole or in part, because the depression of the southern portion of the continent of Europe had not yet begun.

Survivals.—The mammals occurring in these Older Diluvial sands and gravels include several Pliocene survivals from the First Interglacial Stage, associated with the etruscan rhinoceros (*Dicerorhinus etruscus*). If Montmaurin belongs to this stage we may include *Machærodus*. At Mauer two primitive types of bear, *Ursus arvernensis* and *U. deningeri*, are recorded, also *Trogontherium cuvieri*. The Mauer horse first identified as *E. stenonis* is now referred to *E. mauerensis*.

Among the chief localities where the river deposits containing the mammals referred to the Second Interglacial Stage occur are the following:

⁵⁶ DE SAPORTA, G.: "La Flore des Tufs Quaternaires en Provence." C. R. Sess. Congr. Sci. France. Aix, 1867.

EARLY PHASE. WARM FAUNA.

Mauer Sands (Lower), near Heidelberg, Germany. Warm Fauna.
 Montmaurin (Haute Garonne), Pyrenees, France.
 St. Roche, France.

MIDDLE PHASE.

Mosbach, near the Neckar in northern Baden (Fig. 9, 12).
 Süssenborn, near Weimar, Germany (11).

LATER PHASE. COLD TUNDRA FAUNA.

Mauer Sands (Upper), near Heidelberg, Germany (14). Cold Fauna
 approaching the Third Glacial Stage.

Extinctions.—The mammals of this grand life zone have lost nearly all resemblance to those of Upper Pliocene times with the exception of the survival of the etruscan rhinoceros and possibly of the sabre-tooth tiger. The polycladine deer of Upper Pliocene times and of the Norfolk Forest Bed, or First Interglacial, have vanished; neither are there any traces of the axis deer (*C. axis*).

Arrivals.—The Second Interglacial Stage is readily distinguished both in France and Great Britain by a number of important new arrivals, chief among which are the "old elephant" (*E. antiquus*) and the broad-nosed rhinoceros (*D. merckii*). Another very important arrival is the lion related to the African *Felis leo*. The southern elephant has now certainly passed into the *Elephas trogontherii* stage of Pohlig for the type specimen of this intermediate species occurs at Süssenborn; in fact, this is the "*E. trogontherii* stage" of Pohlig; it is also known as the "older *E. antiquus*" stage by Schmidt and other authors. The southern mammoth *E. (meridionalis) trogontherii* is replaced by the more progressive and typical *E. trogontherii*. The broad-faced moose (*Alces latifrons*), the giant deer (*Megaceros*) and the roe deer (*Capreolus*) are all present in the cooler and forested phases of this interglacial period. The true stag (*Cervus elaphus*) is certainly recorded. The cattle (*Bos primigenius*) begin to be numerous and the bison (*Bison priscus*) also appear in numbers. Horses of larger size occur (*E. mosbachensis*, *E. süssenbornensis*).

Among the river-living forms are the beavers (*Castor*). The giant beaver (*Trogontherium*) is by some authors said to make its last appearance in Europe in this sub-stage, but it is again recorded in the Third Interglacial at Chelles. Other rodents include the marmots (*Marmotta*) now found in the Alps, Carpathians and Pyrenees, whose remains may have been borne down by the streams. Beside the lions the carnivores include the typical Eurasiatic forest forms, namely, the lynx (*F. lynx*), two varieties of bear (*U. deningeri*, *U. arvernensis*), and the badger (*Meles*).

The chief components of the fauna of the Second Interglacial Stage

are seen to belong, first, to the Eurasiatic Forest and Meadow Fauna, only separated by specific and sub-specific differences from the Prehistoric Fauna of Europe; second, to the surviving African-Asiatic fauna, including the hippopotamus, two very distinct kinds of elephant, and two rhinoceroses; third, there is evidence in the late colder phases of this period of the first occurrence in Europe of the Tundra Fauna as represented by the reindeer (*Rangifer tarandus*). This animal is recorded in the gravels of Süssenborn by Weiss. Hilzheimer⁵⁷ also speaks of the remains of reindeer as occurring both in Süssenborn and Steinheim in association with the remains of *E. trogontherii*. This author regards *E. trogontherii* from the structure of its grinding teeth as analogous in habit to the Asiatic elephant which inhabits the forests of India, and believes that the presence of this animal indicates a relatively moist climate and well forested country.

AFRICAN-ASIATIC TYPES

Primates

Homo heidelbergensis

AFRICAN-ASIATIC FAUNA

Straight-tusked elephant

E. antiquus

Trogontherian mammoth

E. trogontherii

Broad-nosed rhinoceros

D. merckii

Etruscan rhinoceros

D. etruscus

Hippopotamus

H. major

(?) Sabre-tooth tiger

Machærodus

Lion

Felis leo spelæa

EURASIATIC HARDY FAUNA

Urus

Bos primigenius

Bison

Bison priscus

Stag, roe deer, moose, giant deer

Bear, lynx, badger, wild cat

(Late)

Reindeer

Rangifer tarandus

In this assemblage it is noteworthy that the Eurasiatic Forest and hardy temperate types greatly predominate over the African-Asiatic types. This is another indication that the climate was of a warm-temperate character rather than such as now characterizes southern Asia and Africa. It follows that all the African-Asiatic mammals may have been well protected by hairy covering and adapted to a temperate climate.

In the caverns near Montmaurin in the Pyrenees⁵⁸ we find remains of an early Pleistocene fauna which contains the sabre-tooth tiger (*M. latidens*), the broad-nosed rhinoceros (*D. merckii*), the stag (*C. elaphus*), the brown hyæna (*H. brunnea striata*).

The most typical fauna is that of Mosbach in northern Baden. Here there occur all the characteristic mammalian types of the period, the hippopotamus, the urus, the bison,

⁵⁷ HILZHEIMER, MAX: Handbuch der Biologie der Wirbeltiere, pp. 678-679. Stuttgart, 1912-1913.

⁵⁸ BOULE, M.: "La Caverne à Ossements de Montmaurin (Haute-Garonne)." L'Anthropol., Vol. XIII, pp. 305-319. 1902.

the broad-nosed rhinoceros, two species of mammoth (*E. antiquus*, *E. trogontherii*), and the horse (*E. mosbachensis*).

In the Lower sands of Mauer near Heidelberg there occur the first recorded remains of man and a fauna including some primitive species.

Homo heidelbergensis.—To the faunal stage of *Elephas antiquus* and the etruscan rhinoceros (*D. etruscus*) is to be added the Heidelberg man, determined from a lower jaw discovered by Otto Schötensack⁵⁹ in 1907 in the Lower Mauer Sands at a depth of 24.10 m., one of the most important discoveries in the whole history of anthropology. The lower jaw is exceptionally massive, without chin projection, with a large but essen-



FIG. 14.—Sand pit at Mauer near Heidelberg

The lower jaw (*Homo heidelbergensis*) was found at the spot marked with a cross.
After Schoetensack and MacCurdy.

tially human set of teeth; in other words, it is a jaw in some respects similar to that of an anthropoid ape but containing the dentition of a man, namely, typically human canine and molar teeth. The jaw is now regarded by anatomists as resembling on a very massive and primitive scale the jaw of the neanderthaloid human type (*Homo neanderthalensis*) which first occurs in the Third Interglacial Stage.

The fauna associated with *Homo heidelbergensis* is of an ancient char-

⁵⁹ SCHÖTENSACK, OTTO: Der Unterkiefer des *Homo heidelbergensis* aus den Sanden von Mauer bei Heidelberg: Ein Beitrag zur Paläontologie des Menschen. Verlag von Wilhelm Engelmann. Leipzig, 1908.

acter. Schötensack likened it to that of the First Interglacial or Norfolkian Stage. The presence of the etruscan rhinoceros would appear to justify this opinion, but it is overborne by the similarity to the fauna of Mosbach including the presence of *Equus mosbachensis*, a species highly characteristic of the Second Interglacial Stage. The entire fauna of these Lower Sands of Mauer is now identified (Schmidt, 1912), as follows: *Elephas antiquus*, *D. (Rhinoceros) etruscus*,⁶⁰ *Equus mosbachensis*, *Sus scrofa feræ*, *Alces latifrons*, *Cervus elaphus*, *Capreolus capreolus*, *Bison priscus*, *Bos primigenius*, *Ursus arvernensis*, *U. deningeri*, *Felis leo*,⁶¹ *Felis catus*, *Canis neschersensis*, *Castor fiber*. The enumeration of

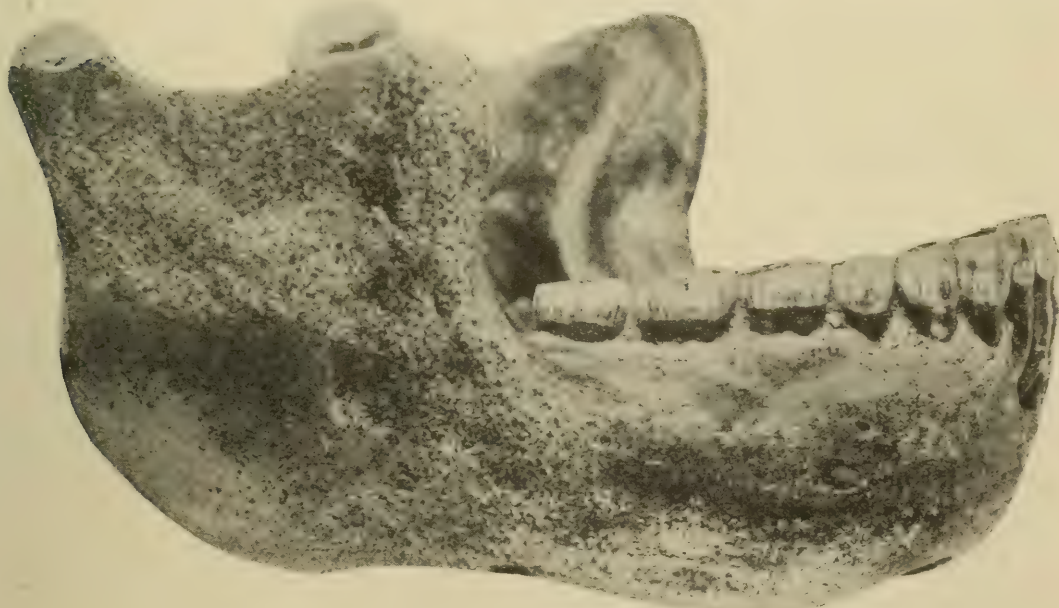


FIG. 15.—Heidelberg jaw

The human lower jaw ($\frac{3}{4}$ natural size) found near Heidelberg, on which is based the species *Homo heidelbergensis*. After Schoetensack.

this fauna is very important as indicating the temperate climatic conditions which surrounded the Heidelberg man. Wurm observes that the Etruscan rhinoceros only occurs in Mauer and that its variations indicate a transition towards the *D. merckii* which occurs at Mosbach and Süssenborn but not in Mauer. Above this layer occurs a deposit of the "Older Loess," indicating an arid climate. The Upper Sands of Mauer contain a cold fauna which by some is referred to the close of the Second

⁶⁰ WURM, A.: "Über *Rhinoceros etruscus* Falc. von Mauer a. d. Elsenz (bei Heidelberg)." Verh. d. Naturhist.-Medizin. Vereins zu Heidelberg, N. F. XII Band, 1 Heft, pp. 1-62, pll. I-IV. 1912.

⁶¹ WURM, A.: Beiträge zur Kenntnis der Diluvialen Säugetier fauna von Mauer a. d. Elsenz (bei Heidelberg), I. *Felis leo fossilis*. Jahresberichte und Mitteilungen des Oberrhein. geol. Vereins, N. F., Bd. II, Heft 1, pp. 77-102. 1912.

Interglacial stage, by others (Wurm,⁶² 1913, p. 68) to the "Younger Loess," that is, to the Fourth Glacial or Postglacial Stage.

CHELLEAN CULTURE WITH ANCIENT INTERGLACIAL FAUNA

In favor of the antiquity of the Chellean culture may be urged the fact of its association in several localities (Torralba, Abbeville, Piltown) with the primitive mammals identified as *Machærodus*, *D. etruscus*, *Equus stenonis*. The specific identifications may be incorrect, but these Pliocene species are characteristic of the Second Interglacial Stage and are not certainly recorded in the Third Interglacial Stage of northern Europe at least. For example, at Torralba, Province of Soria, Spain, there has been discovered (Harlé, 1910, p. 75) an old typical Chellean camping site containing abundant remains of *D. merckii* and *E. meridionalis* (*trogontherii*) mingled with remains of other mammals of primitive type identified as *Dicerorhinus etruscus* and *Equus stenonis*. These associations with Chellean remains tend to support the theory that the Chellean culture began during the Second Interglacial Stage. Another very ancient fauna associated with very primitive Chellean or pre-Chellean implements is that found near Abbeville, Gisement de Champ de Mars.⁶³ Beside typical members (such as *E. antiquus*, *E. meridionalis trogontherii*, and *D. merckii*) of warm Second Interglacial times this fauna is said to contain such primitive types as *Trogotherium*, *D. etruscus*, *Equus stenonis*, also very numerous specimens of *Machærodus* and *Hyæna brevirostris*.

We cannot fully agree with Schmidt (1912) when he observes that the faunal separation of the Acheulean and Chellean is not so marked that we are obliged to separate these cultures by a long period of time.

FAUNA OF THE PYRENEES, CANTABRIAN ALPS, SPAIN AND PORTUGAL ⁶⁴

The entire warm fauna characteristic of Germany, Great Britain and France also penetrated the Cantabrian Alps, Spain and Portugal as far south as Gibraltar.

A macaque (*Macacus*) related to the Algerian species occurs in the grotto of Montsauné (Haute Garonne) associated with the hyæna (*H.*

⁶² WURM, A.: "Über eine Neuentdeckte Steppenfauna von Mauer an der Elsenz (bei Heidelberg)." Jahresber. u. Mitt. d. Oberrhein. geol. Vereins, N. F., Bd. III, Heft 1, pp. 62-78, pl. vi. 1913.

⁶³ D'AULT DU MESNIL, G.: "Note sur le Terrain Quaternaire des Environs d'Abbeville." Revue Mensuelle de l'École d'Anthropologie de Paris, VI year, pp. 285-296. 1896.

⁶⁴ HARLÉ, EDOUARD: "Les mammifères et oiseaux quaternaires connus jusqu'ici en Portugal. Mémoires suivi d'une liste générale de ceux de la Péninsule Ibérique." Commun. du Service Géol. du Portugal, T. viii, pp. 22-85, pl. I-V. 1910.

striata), with a dhole (*Cyon*), and other members of the warm fauna of *E. antiquus* and *D. merckii*. The porcupine (*Hystrix cristata*) also occurs here.

The striped hyæna (*H. striata brunnea*) is associated with *Machærodus latidens* in the cavern of Montmaurin (Haute Garonne). The striped hyæna occurs at five other localities in the Pyrenees, Spain and Portugal (Furninha); it has also been recognized in Germany (Mosbach), Austria (Hundsheim) and France (Harlé, 1910, p. 40); it disappears later or retires to the south, while the spotted hyæna (*H. crocuta spelæa*) becomes adapted to the extreme cold and survives with the reindeer to the end of Postglacial times. The Carnivora of this region are *Felis leo spelæa*, the panther (*Felis pardus*), the wild cat (*Felis catus*), and the lynx (*Felis pardina*).

SECOND AND THIRD GLACIAL AND INTERGLACIAL EPOCHS

AFRICAN-ASIATIC FAUNA

Four great animals especially characterize this fauna: *Elephas trogontherii* and *Hippopotamus major*, *Dicerorhinus merckii* and *Elephas antiquus*.

Old Elephant (*Elephas antiquus*).⁶⁵—The "old elephant" or straight-tusked elephant (*Elephas antiquus*) does not occur in France or Great Britain until the Second Interglacial Stage, but it is said to occur in the Arno valley of Italy during an earlier stage in which it is associated with a warm fauna including the southern mammoth and the hippopotamus. The typical *E. antiquus* is recognized by its narrow, elongated grinding teeth with comparatively few plates which, combined with its skull characters, suggest its affinity to the modern African (*Loxodonta*) rather than to the Indian elephant (*Euelephas*) group. While during the first, or Norfolk, interglacial period it is confined to Italy, in subsequent interglacial times it wandered into northern Europe as one of the grandest and most distinctive forms, attaining a very wide distribution. Pohlig certainly overestimates its size⁶⁶ in assigning to it a height of 5 m. at the back (16 ft. 8 in.), or 1 m. more than the mammoth, and with tusks also 5 m. in length. In consequence of the size and weight of the tusks, the head, shoulders and fore legs were enormously developed. The same writer believes that the habitat of this mammoth retreated and advanced

⁶⁵ POHLIG, H.: "Dentition und Kraniologie des *Elephas antiquus* Falc. mit Beiträgen über *Elephas primigenius* Blum. und *Elephas meridionalis* Nestl." Nov. Act. Ksl. Leop.-Carol. Deutsch. Akad. Naturforsch., Vol. LIII, No. 1, p. 326. Halle, 1888.

⁶⁶ POHLIG, H.: Eiszeit und Urgeschichte des Menschen. Leipzig, 1907.

with the successive ice waves and warm interglacial times. Because of the resemblance of the grinding teeth of *E. antiquus* to those of the African elephant (*L. africanus*) it has been assumed perhaps too readily that this ancient elephant was characteristic of a tropical climate. It resembles the African elephant in the prominence of the enamel bands of the grinding teeth, which are adapted to the comminution of twigs and woody food, which justifies the belief that this animal frequented the forests. For these reasons Hilzheimer regards *E. antiquus* as indicative of forest conditions.

Rhinoceroses.—The three great rhinoceroses characteristic of the European Pleistocene are each of distinct geological value. In general *D. etruscus* belongs to the First Interglacial Stage, *D. merckii* characterizes the Second Interglacial Stage and most of the Third Interglacial, while *D. antiquitatis* is distinctive of the Fourth Glacial and the Post-glacial.

The two species first named are apparently related to the Sumatran phylum (*Dicerorhinus sumatrensis*). The *D. etruscus* of the Val d'Arno, of the First Interglacial and of the early phases of the Second Interglacial is a relatively small animal, distinguished by brachyodont grinding teeth and long, slender limbs, a small anterior and a larger posterior horn. It is remotely related to the Sumatran rhinoceros but differs in the absence of cutting, or incisor teeth. It is essentially a browsing type. Its remains in Mauer are said (Wurm, 1912) to afford a transition to *D. merckii*.

Related to this animal in the Second Interglacial Stage in Great Britain, Germany, France, Italy, there appears the broad-nosed rhinoceros known as *D. megarhinus*, or *D. merckii*. It resembles *D. etruscus* in its smaller anterior and larger posterior horn and in the elongation of its limbs and feet, but differs from it in the possession of relatively long-crowned (hypsodont) grinding teeth adapted to grazing habits. This animal is very widely distributed geographically in the Second and the first half of the Third Interglacial Stage, and is in most localities associated with remains of the hippopotamus and "old elephant."

Quite distinct from these animals is the woolly rhinoceros (*Diceros antiquitatis*, *D. tichorhinus*) which belongs with the colder climates of tundra and steppe conditions and is almost invariably associated with remains of the true woolly mammoth (*E. primigenius*). Like the above described Sumatran species it lacks the front, or cutting teeth and has in consequence been improperly considered as related to *Dicerorhinus*, but really belongs to the modern African group of *Diceros*, resembling especially the species *D. sinus*, with which it closely agrees in its dolicho-

cephalic cranial proportions, its long-crowned teeth, and especially in the presence of a square upper lip and very large anterior horn and small posterior horn. It is thus distinguished both by the proportions of its horns and by the characters of its teeth and lips from the two species of *Dicerorhinus*. It is distinctively a grazing animal.

SYNONYMY OF RHINOCEROS GENERA

1. Indian rhinoceros: *R. indicus* = RHINOCEROS Linnæus 1758
2. Black rhinoceros of Africa: *D. bicornis* = DICEROS Gray 1821
3. Woolly rhinoceros: *R. antiquitatis* (Blumenbach 1799) = CÆLODONTA Bronn 1831
4. Sumatran rhinoceros: *D. sumatrensis* = DICERORHINUS Gloger 1841
5. White rhinoceros of Africa: *D. simus* = CERATORHINUS Gray 1867

The names of these three rhinoceroses are almost hopelessly confused in the early literature. The animals converge toward each other in several characters, namely, in the loss of cutting teeth and in the development of an osseous septum for the support of the nasal bones. The woolly rhinoceros (*D. antiquitatis*) is first recorded in Europe in deposits correlated with the Third Glacial or Riss Stage, the Mammut Lehm of Cannstatt (Koken, Schmidt, 1912).

Bovines.—The bison (*B. priscus*) rivalled the mammoth as a wanderer and was able to adapt itself to wide diversities of climate in Europe, Asia and America. Originally of African-Asiatic origin it became thoroughly acclimated as a Eurasiatic meadow and plains type and may have extended also into the forests like the existing woodland bison (*B. athabascæ*) of Canada. It is readily distinguished as brachycephalic while its contemporary, the gigantic urus, is long-headed (dolichocephalic), as well as less agile than the bison. In external appearance, as depicted in the very numerous engravings and paintings in the Font de Gaume and other caverns, this animal resembled the existing American bison (*B. americanus*) more than the still surviving Lithuanian and Caucasian form (*B. bonasus*). The animal appears in the First Interglacial, or Norfolkian Stage in France. In the Second long warm Interglacial Stage there existed a bison (*B. priscus antiquus*) which enjoyed a wide distribution. The animal found its way to the Mediterranean islands and gave rise to the pigmy varieties.

The wild ox (*Bos primigenius*) also occurs in the First Interglacial Stage and survived the vicissitudes of the entire Pleistocene Epoch. The "urus" of Cæsar survived in its wild state in Europe as late as the seventeenth century A. D., where it was still to be found in the forests of Poland and in a few game preserves. It then disappeared so completely

that even its popular designation "auerochs" was transferred to the Lithuanian bison.⁶⁷ The designations of these two types are therefore very confusing and are distinguished by Kobelt as follows:

Urus (Pliny),	wild ox, urochs, auerochs (Old German), tur (Polish), urstier	= <i>Bos primigenius</i>
Bonasmus (Aristotle)	wisent or wisont, subr (Polish), auerochs (of recent date)	= <i>Bos priscus</i>

The relations of the wild cattle of Asia to domestication will be considered on a later page.

Megaceros giganteus.—During the first half of the Pleistocene this noble animal was widely distributed in Ireland, England, Scotland, the Isle of Man, France, Denmark, Germany, Austria, northern Italy and parts of Eurasia even into Siberia. The famous *Megaceros* beds of Ireland are freshwater clays which frequently underly the peat bogs. As observed by Williams these are "boulder-clays" which were redistributed as lake sediments and accumulated under genial or temperate climatic conditions like the present. Owing to the similarity in the palmation of its antlers the giant deer has been generally (Lydekker, Weber, Trouessart) placed within or very close to the subgenus *Dama*, the fallow deer; but Lönnberg⁶⁸ regards the likeness between the giant deer and fallow deer as convergence and considers that the giant deer is more closely related phylogenetically to the reindeer, but it is nevertheless so specialized as to hold an independent place in the system of Cervidæ. The *Megaceros* last appears in early Postglacial times associated with the Aurignacean culture in Germany; it is not recorded (Schmidt) with the succeeding Solutrean or Magdalenian culture. It thus became extinct before the close of the Palæolithic.

Elaphine or Red Deer.⁶⁹—Sir Victor Buck held that the Cervidæ originated in Asia and from there spread westward into Europe or eastward into America. The Asiatic origin of the red deer race has since been ably maintained by Köppen. A very large race of late Pleistocene times has been compared by Nehring with the *C. canadensis* of North America.

Reindeer.—The reindeer of Pleistocene times are generally referred to the Barren Ground or Tundra type. In this type, which is typified by the existing Old World reindeer (*R. tarandus*, *R. spitzbergensis*) and by the American arctic forms (*R. arcticus*, *R. Grœnlandicus*, *R. granti*, *R.*

⁶⁷ POHLIG, H.: *Eiszeit und Urgeschichte des Menschen*, p. 131. Leipzig, 1907.

RÜTIMEYER, L.: "Die Fauna der Pfahlbauten der Schweiz." *Neue Denkschr. schweiz. Ges. gesam. Naturwiss.*, Vol. xix, pp. 68-112. Zürich, 1862.

KOBELT, W.: *Die Verbreitung der Tierwelt*. 8vo. Leipzig, 1902.

⁶⁸ LÖNNBERG, E.: "Which is the Taxonomic Position of the Irish Giant Deer and Allied Races?" *Ark. Zoöl.*, Vol. 3, No. 14, pp. 1-8. Upsala, 1906.

⁶⁹ SCHARFF, R. F.: *The History of the European Fauna*, pp. 246-251. London, 1899.

pearyi), the antlers are round, slender and long in proportion to the relatively small size of the animal, while the spreading beam and brow tines are as a rule but little palmated, although in some forms the brow tine is palmated.

The woodland type, which is now extinct in Europe, is typified by several American species⁷⁰ (*R. caribou*, *R. montanus*, *R. osborni*) in which the antlers are heavier, flatter, thicker, and more heavily palmated on the spreading beam and on the "brow tine" especially, while the tine above the brow, which corresponds to the bez-tine of the stag (*Cervus*), is elaborately developed and palmated thus contrasting sharply with the simple bez-tine of the Barren Ground group.

Some writers⁷¹ (Scharff) maintain that the Barren Ground reindeer entered Europe first during the First and Second Glacial Stages while the woodland group first appears in the Third Glacial Stage. Others (Hilzheimer) maintain that all the known Pleistocene reindeer belong to the Tundra form and not to the woodland form. Again, Dietrich⁷² recognizes a woodland caribou in the "high terrace" gravels of Steinheim in the valley of the Murr.

Carnivores.—The larger Pleistocene carnivores embrace the wolves (*Canis lupus*), the bears (*U. arctos*, *U. spelæa*), the hyænas (*H. crocuta spelæa*, *H. (brunnea) striata*), the leopards (*Felis pardus* of Spain) and the lions.

The chief enemies of the wild horses and cattle of the Pleistocene were the lions (*Felis leo spelæa*), descended either from the great cats of the Pliocene of France and Italy (*Felis arvernensis*) or more probably migrants from northern Africa. These lions are known from deposits in England, Belgium, Austria, southern Russia, France, Spain,⁷³ Italy, Sicily, Greece and Algeria.⁷⁴ The fact that remains of this animal are so often associated with those of the cold Postglacial fauna makes Nehring's⁷⁵ suggestion seem plausible that the cave lion was a northern race of the recent African and western Asiatic lion adapted to a colder climate and with a heavy coat. After examination of specimens from central and northern Europe Boule⁷⁴ reaches the conclusion that these lions

⁷⁰ GRANT, MADISON: "The Caribou." Ann. Rept. N. Y. Zoöl. Soc., no. 7, pp. 175-196. New York, 1892.

⁷¹ *Op. cit.*, p. 154.

⁷² DIETRICH, W. O.: "Neue fossile Cervidenreste aus Schwaben," Jahreshefte des Vereins f. vaterländische Naturkunde, Jahrg. 66, pp. 320-336. 1910.

⁷³ HARLÉ, EDOUARD: "Les mammifères et oiseaux quaternaires connus jusqu'ici en Portugal. Memoires suivi d'une liste générale de ceux de la Péninsule Ibérique." Commun. du Service géol. du Portugal, T. VIII, pp. 22-85, pll. I-V. 1910.

⁷⁴ BOULE, MARCELLIN: "Les Grands Chats des Cavernes." Ann. de Paléont., Vol. I, pp. 20-27. Jan., 1906.

⁷⁵ NEHRING, A.: Über Tundren und Steppen der Jetzt-und Vorzeit, mit besonderer Berücksichtigung ihrer Fauna. Berlin, 1890.

are not related to the tiger (*F. tigris*) as was supposed formerly by De Blainville and Lartet. While rich in individual variations *Felis leo spelæa* is nearer the lion than the tiger in most of its characters; it should, in fact, be considered a veritable race of the recent lion with the name *Felis leo spelæa*. It differs from both the recent lion and tiger in the more gentle and uniform slope of its facial profile and in its large, flat forehead, but its limb bones are longer and proportionately thicker. It sometimes equals and often surpasses the existing lions and tigers in size. It is represented in the cave engravings and drawings both of early and late Postglacial times.

The cave hyæna (*Hyæna crocuta spelæa*) is a variety of the living spotted hyæna (*Hyæna crocuta*) of East Africa, but it attained dimensions considerably greater than that of its living ally. It has the larger proportions, the heavier build, the broad skull, the powerful carnassial teeth which distinguish the spotted from the striped hyæna (*H. striata*) of the present day. Although proportionately heavier the hind limbs may have been shorter than in the spotted hyæna in adaptation to the cavern life which the inclement climate made necessary. The cave hyæna was a very abundant type and is responsible for scattering of the vast numbers of the bones of the contemporary animals in a manner not pleasing to the palæontologist.

In the caves of southern France a variety (*Hyæna priscus*) of the striped hyæna (*Hyæna striata*) also occurs and there are also discovered here additional remains of an animal (*H. intermedia*) resembling the cave hyæna. Thus the Pleistocene species of European hyænas underwent an evolution of their own. As a result the living African forms differ more from the Pleistocene hyænas of Europe than they do from those of Pliocene times.

Harlé⁷⁶ records the striped hyæna (*H. striata*) as characteristic of the earlier or warm Pleistocene of Spain and Portugal; the cave hyæna (*H. crocuta spelæa*) survived into the late Pleistocene through adaptation to the cold climate.

The cave wolf (*Canis lupus spelæa*), a member of the forest fauna, also attained dimensions greater than its living allies. According to Gaudry and Boule,⁷⁷ (1892) no constant osteological differences can be determined between the Pleistocene cave wolf and the modern wolf of western Europe, although the cave form is of considerably larger size. This animal is represented in the Upper Magdalenian paintings of Font de Gaume.

⁷⁶ *Op. cit.*, 1910. pp. 46, 70.

⁷⁷ GAUDRY, A., and BOULE, M.: Matériaux pour l'Histoire des Temps Quaternaires. Fasc. 4. Les Oubliettes de Gargas. pp. 108-112. Paris, 1892.

THIRD GLACIAL STAGE—ILLINOIAN, POLANDIAN, RISS

In North America the Third Glacial Stage is heralded by the advance of a great ice cap radiating from Labrador which sent its glaciers to the south and far southwest, depositing the Illinoian drift which is regarded (Leverett, 1910, p. 315) as of an earlier period than the Polishian or "Middle Drift" of northern Germany or the Riss drift of the Alpine region. This Third glaciation of the Alpine region has a period of advance and retreat which is relatively estimated by Penck at 20,000 years, the snow line descending 1,250m. With it are associated the "high terrace" deposits of the Alpine region. The Third glaciation was greatly extended along the Rhine, in parts of Switzerland, in France, and in the valley of the Po (Fig. 9). In northern Germany the principal reason for separating the "Middle Drift" (Polishian) from the "Upper Drift" (Mecklenburgian) is the presence of loess deposits between them which seems to strengthen the evidence for a Third Interglacial interval. These loess deposits are regarded by certain German geologists (Koken) as the continuation of the "Older Loess" but by Penck and Leverett they have been regarded as belonging to the "Newer Loess."

THIRD GLACIAL FAUNA

The recurrence of a cold climate in Germany is heralded in the Upper Sands of Mauer by the arrival of the reindeer and other arctic types. In the Mammut Lehm of Cannstatt is found a fauna which is regarded by Koken and Schmidt (1912, *op. cit.*) as contemporaneous with the Third Glacial advance. It is noteworthy as containing two new arrivals from the tundras of the north, namely, the woolly mammoth (*E. primigenius*) and woolly rhinoceros (*D. antiquitatis*), as well as the reindeer (*R. tarandus*). The other members of this fauna include two species of horse, the giant deer, the stag, the bison and the urus. "Cannstatt," observes Schmidt (1912, p. 270), "affords a geological and final connecting link between the Second Interglacial fauna of Mauer and the fauna of Early Palæolithic [or Third Interglacial] times." If this fauna actually entered Germany during the cold period of the Third glaciation it returned to the north with the approach of the warm-temperate climate of the Third Interglacial Stage, because no trace of it is found until near the close of the Third Interglacial Stage.

THIRD INTERGLACIAL STAGE—RISS-WÜRM, SANGAMON

The Third Interglacial Stage is shorter than the Second, its geologic and faunal characters are more fully known, and it embraces the first

undoubted remains of human stone industry in Europe as well as abundant remains of man. In the Alpine region this Riss-Würm Stage is indicated by "high terraces," which rise 25 to 50m. above the existing streams. The Riss-Würm interval is evidently shorter than that between the Second and Third glaciation. Penck considers that the depositions of "Newer Loess" which occurred in the Alps near the close of Riss-Würm Interglacial times represent a cold stage, since the fauna which it contains is of the Tundra-Alpine type and the Palæolithic implements found in it are closely similar in workmanship to those found in deposits subsequent to the Würm glaciation (Penck, 1909, p. 1159). He regards this as the "Newer Loess" that was laid down prior to the Fourth glaciation. Koken and Schmidt, on the other hand (1912), regard the "Newer Loess" as partly or wholly Postglacial, that is, as occurring after the Würm maximum. The Third Interglacial loess of northwestern Europe was comparatively scanty and discontinuous, from 1 to 5m. in thickness, and contains a terrestrial molluscan fauna as in America. All the indications are that this loess was deposited by prevailing westerly winds. Also along the Danube the loess is chiefly due to westerly winds. Penck attributes the scarcity of loess in the southern, eastern and western borders of the Alps to the presence of thick vegetation even during the glacial stages, the moraines being pushed out into the forests.

In America the Third Interglacial interval is known as the *Sangamon*; the deposits are composed of dark, black soil which is overlain by the main or thickest loess deposit of the central United States. There appears to have been a long interval between the melting of the Third Glacial ice and the deposition of the loess which contains a terrestrial molluscan temperate fauna, indicating climatic conditions not greatly different from those now existing in the same regions (Shimek, 1909).

The geologic deposits of this stage are mainly of three kinds: first, fluviatile sands and gravels; second, loess; third, hearth or kitchen-midden deposits made by man toward the cold closing period of this stage.

CLIMATIC CHANGES DURING THE THIRD INTERGLACIAL STAGE

The Third Interglacial Stage opens with a renewal or continuation of climatic conditions favorable to an Asiatic-African fauna exactly similar to that of the warm Second Interglacial period. This warm fauna is known as the "Second *E. antiquus* fauna." It includes the hippopotamus, the straight-tusked elephant (*E. antiquus*) and the southern elephant (*E. trogontherii*). This last species is even referred to by many writers as *E. meridionalis*.

This is the *Elephas antiquus* Stage of Pohlig, this animal being very abundant until toward the close of the Third Interglacial Stage when it makes its last appearance in Europe. The broad-nosed rhinoceros (*D. merckii*) is also abundant and appears in Europe for the last time.

The successive climatic phases of mammalian life are most clearly recorded in connection with the culture stages of the Lower Palæolithic period, including the pre-Chellean, Chellean, Acheulean, and the beginning of the Mousterian cultures. As indicated on p. 233, the warm Asiatic-African fauna prevails from the pre-Chellean until toward the close of Acheulean times, when there is evidence of the advent of a cold dry continental climate, on the approach of which the hippopotamus, *Elephas antiquus*, and *Dicerorhinus merckii* gradually retreat. Thus at Villejuif, south of Paris, the late Acheulean implements are found imbedded in great drifts of loess, a proof that a cooler, drier climate which marks the transition from the last warm Interglacial Stage to the Fourth Glacial advance was prevalent. Chiefly in the southern parts of France we find the *Elephas antiquus* fauna still persisting until the close of the Third Interglacial Stage or during the early Mousterian period, a sign that this old African-Asiatic stock did not become extinct but migrated from central Europe to warmer regions in the south and southwest.

Flora.—Indications of changes of climate in the Third Interglacial interval are preserved in the *tuf de la Celle-sous Moret* (Seine-et-Marne)⁷⁸ which overlies Pleistocene river gravels near Paris. The lower levels contain the sycamore maple (*Acer pseudoplatanus*), willows (*Salix*), the Austrian pine (*Pinus laricia*). Higher up in the same deposits we find the box tree (*Buxus*) and not uncommonly the fig (*Ficus*); the canary laurel (*Laurus nobilis*) occurs less frequently: the canary laurel and the fig indicate that the winters were mild because both these plants flower during the winter season. The climate was more damp and somewhat milder than that of the present time in this region. The Mollusca of the tufa of *La Celle* also indicate that the climate of northern France was more equable so as to permit species now widely separated to live together. The plants in the highest levels of the tufa, however, indicate a cooler climate and yield *Acheulean* flints. The tufa is itself covered by a sheet of loess corresponding to the return of a cool, arid period in late Acheulean times.

In Lorraine below the level of the fauna of the Fourth glaciation there occurs a flora in which the most northerly varieties of the larch (*Larix*) and the mountain pine (*Pinus lambertiana*) predominate. The lignites of Dürnten and of Utznach near Zürich (Fig. 9, 18) contain fossil re-

⁷⁸ HAUG, *op. cit.*, 1908-11, p. 1812.

mains of forests of Third Interglacial age similar to those which still flourish in the same region, consisting of spruce, fir, mountain pine, larch, birches, yews and sycamores with undergrowth of hazel. These lignitic deposits rest upon the remains of a retreating glacier and are in turn covered with those of another glacier and are therefore interglacial.⁷⁰ With this hardy flora are associated remains of *Elephas antiquus*, *D. merckii*, the urus and the stag.

Fauna.—The mammalian fauna is broadly divided into: first, the warm African-Asiatic, which disappears from Europe at the close of the Third Interglacial Stage; second, the Eurasiatic Forest Fauna, in which we now include the urus (*B. primigenius*) and the bison (*B. priscus*); third, the Tundra Fauna, which retreats after the Third Glacial Stage to reappear with the approach of the Fourth Glacial Stage, when the full tide of Tundra life, including fifteen species of mammals and birds, and the advance wave of Steppe life, including nine species of mammals and birds, first arrive in Europe. The chief localities in which the fauna is recorded are the following:

Warm Stage.	CHELLES, ⁸⁰ ST. ACHEUL, valley of the Somme, northern France. Warm Fauna.
	GRAYS THURBROCK and ILFORD, Essex, England. Warm Fauna.
Cool Stage.	TAUBACH-WEIMAR-EHBINGSDORF-ACHENHEIM, Germany. <i>Acheulean Stage</i> . Temperate Fauna.
	DÜRNEN, UTZNACH, near Zürich, Switzerland (cool flora, fauna).
	LAVISTE, AYGEADES, travertines, Marseilles, France (flora).
	KRAPINA (cavern of), Croatia (fauna and human remains).
Cold Stage.	RIXDORF, near Berlin. Cold fauna.

PILTDOWN MAN, EOANTHROPUS DAWSONI

Fragments of a skull and jaws discovered by Dawson in 1911 near Piltdown, Sussex, have been described by Dawson and Smith Woodward.⁸¹ They were associated in a fluviatile sand layer with a single pre-Chellean flint and remains of deer (? deer), rhinoceros (*D. etruscus* or *D. merckii*), beaver (*Castor fiber*), and hippopotamus. The geologic age is not positively determined by the fauna nor by the nature of the river gravel deposits in which these specimens were found. The associa-

⁷⁰ DAWKINS, W. B. "Classification of the Tertiary Period by Means of the Mammalia." *Quart. Jour. Geol. Soc.*, Vol. xxxi, pp. 379-405. Aug., 1880.

⁸⁰ The Chellean culture is placed by Penck and Geikie in the Second Interglacial Stage.

⁸¹ DAWSON, CH., SMITH-WOODWARD, A., SMITH, G. ELLIOT: "On the Discovery of a Palæolithic Human Skull and Mandible in a Flint-bearing Gravel Overlying the Wealden (Hastings Beds) at Piltdown, Fletching (Sussex). With an Appendix by Prof. Grafton Elliot Smith." *Quar. Jour. Geol. Soc.*, Vol. 69, pp. 117-151. Pls. XV-XXI. London, 1913.

tion of the pre-Chellean flint and of numerous Chellean flints in the overlying layer would tend to determine the age as either Third Interglacial or at the earliest Second Interglacial.

The placing of the skull and jaws together as belonging to one individual is not certain, but is highly probable. The cranial bones are extremely thick; the skull is not Neanderthaloid, but is of a high, dolichocephalic type, with a brain capacity variously estimated at 1,100ccm. (Elliot Smith, 1913) to 1,500ccm. (Keith, 1913).^{81a} The jaw resembles closely that of an orang (*Simia satyrus*); the two lower molar teeth preserved are more elongated than in any human type; the superior canine tooth (mistaken by the authors for an inferior canine) resembles that of the anthropoid ape. Thus the specimen may be concisely described as possessing the skull of a man combined with the jaw and the dentition of one of the higher anthropoid apes. A number of eoliths and one palæolith were also found in the same layer with the skull.

PRE-CHELLEAN AND CHELLEAN FAUNA

The dawn of the stone industry in Europe is known as the pre-Chellean. It is found at Chelles in France, in Spain and at Piltdown, Essex, England. It is important to note that the Chellean culture stage is regarded by Penck, Geikie and others as belonging to Second Interglacial times, or the Mindel-Riss, while Boule, Haug, Obermaier, Breuil and Schmidt assign the pre-Chellean-Chellean culture to the Third Interglacial Stage. While the latter opinion generally prevails among archæologists there is reason for further investigation before the geologic age of the pre-Chellean and Chellean cultures can be considered as definitely determined.

The faunal period of the Chellean culture proper is shown in the valleys of the Somme and of the Marne where mingled with the Pre-Chellean and Chellean flints are found the hippopotamus, the southern elephant (*E. meridionalis trogontherii*) with the straight-tusked elephant (*E. antiquus*) and the broad-nosed rhinoceros (*D. merckii*). The typical site of the Chellean culture stage is near the town of Chelles in the wide expanse of the Marne valley. The river deposits of the period of the Chellean culture in this valley are eight meters in thickness and contain beside the animals named above the giant beaver (*Trogontherium*), species of bear, of hyæna, various kinds of deer, larger and smaller kinds of wild cattle and a primitive wild horse.

At Abbeville, at the mouth of the Somme, are found remains of the

^{81a} The corrected and final determination is at 1,300ccm., Smith-Woodward, McGregor.

same animals associated with those identified as belonging to the sabre-tooth tiger (*Machærodus*).

Chellean Culture on the "Low Terraces."—It appears that the Chellean culture stage in many regions was subsequent to the formation of the terraces; thus Chellean flints may occur in the superficial gravels both on the "middle" and on the "low terraces." Haug (1912) supports the theory that the Chellean culture belongs to the Third Interglacial Stage. This accords with the terrace chronology. The minute researches of Laville in the basin of Paris are confirmed by the observations of Commont in the valley of the Somme. Along the Somme Chellean flints occur in the deep gravels overlying the middle and upper terraces. The fauna found in the "low terraces" of Chelles and of Grenelle is the same, namely, *E. trogontherii*, *Trogontherium cuvieri*, *Hyæna crocuta*, *D. merckii*, *Hippopotamus major*, *Elephas antiquus*. All these animals found at Chelles occur in the gravels a few meters above the level of the Marne; they belong exclusively to the sands and gravels at the base of the diggings in the "low terrace." Similarly in the valley of the Somme near Abbeville from the base of the "low terrace" are recorded Acheulean flints with *H. major*, *D. merckii*, *Elephas antiquus*, etc. Laville collected at Arceuil in the valley of the Bièvre, in gravels assigned to the "low terrace," Chellean, Acheulean and Mousterian flints; these "low terraces" are only 5m. above the river level and are still occasionally flooded with the high waters of the Seine. It is hardly probable that the close geologic and faunistic association of the Chellean-Acheulean cultures in these "low terraces" could have been separated by a very long geologic period, amounting to a hundred thousand years, as demanded by the theory of Penck.

What is regarded as the typical Third Interglacial fauna of the more northern regions of Europe as found at Grays Thurrock, Ilford (Essex, England) and at Taubach is as follows:

Straight-tusked elephant, *Elephas antiquus*
 Southern mammoth, *E. trogontherii*
 Broad-nosed rhinoceros, *D. merckii*
 Hippopotamus, *H. major*
 Wild horse, *E. ? caballus* (probably the Forest variety)
 Wild boar, *Sus scrofa ferus*
 Bison, *Bison priscus*
 Urus, *Bos primigenius*
 Red deer, *Cervus elaphus*
 Roe deer, *C. capreolus*

Grays Thurrock, Ilford (Essex, England).—The hippopotamus is here recorded by Dawkins. The elephant of Essex is referred by Pohlig to *E. trogontherii*. The horse (Ewart) is considered to belong to the Forest or Nordic type. This Essex fauna is characteristic of the river shores and of the neighboring forests and meadows. The lions, hyænas and bears which are re-

Giant deer, *Megaceros*
 Hyæna, *H. crocuta spelæa*
 Brown bear, *Ursus arctos*
 Wild goat, *Capra*
 Lion, *Felis leo antiqua*
 Wolf, *Canis suessi*
 Badger, *Meles taxus*
 Marten, *Mustela martes*
 Otter, *Lutra vulgaris*
 Beaver, *Castor fiber*
 Hamster, *Cricetus vulgaris*
 The water vole, *Arvicola amphibius*

corded here are not true cave types, but are in part ancestors of the cave types which appear in the succeeding reindeer or cavern period.

ACHEULEAN CULTURE FAUNA

Warm Stage.—The early Acheulean culture as found at Taubach, Weimar, Ehringsdorf and Achenheim contains the hippopotamus and the straight-tusked elephant (*E. antiquus*). The principal feature of the early Acheulean culture stage seems to be the abundance of these African-Asiatic animals so that this is commonly known as the “warm Acheulean” fauna.

Cool Stage.—The Acheulean culture endured for a long period of time and toward its close two typical members of the warm fauna, namely, the hippopotamus and *E. trogontherii*, disappear. Thus the late Acheulean fauna does not include either hippopotamus or *E. trogontherii* but there still survive the *E. antiquus* and the broad-nosed rhinoceros (*D. merckii*). These animals persisted in Europe for a considerable time and becoming adapted to a colder climate are sometimes found in association with the advent of the true mammoth (*E. primigenius*) and the woolly rhinoceros (*D. antiquitatis*).

During late Acheulean times a dry, cool continental climate prevailed (Hilzheimer, 1913, p. 145) similar to that of the steppes of southern Russia between the Ural Mountains and the Caspian Sea. Evidences of this are observed even in the sheltered valley of the Vézère, a tributary of the Dordogne in southwestern France. Similarly as regards north-central France, Obermaier (1912, pp. 122-124) observes that while the climate was mild and temperate and the country still forested at the beginning of the Acheulean culture, in late Acheulean times the implements at Villejeuf south of Paris, are found embedded in drifts of loess, a proof that the colder climate which marks the transition from the Third Inter-glacial Stage to the Fourth Glacial Stage was now beginning to prevail. The fauna is still that of *E. antiquus* and *D. merckii*. More rarely (Schmidt, 1912) Acheulean palæoliths are associated even with remains

of the woolly mammoth and the woolly rhinoceros, indicating that in northern localities the Acheulean culture reached the cold period of the Fourth Glacial Stage.

Krapina Neanderthaloid Race.—To the Acheulean Stage there is referred a human tooth found at Taubach. Of much greater importance is the presence of abundant skeletal remains of men of a primitive Neanderthaloid race found in the cave-shelter of Krapina in Croatia. These remains are positively associated with the Acheulean stage by Schmidt (1912, p. 256) but they are regarded as more recent, of the late Mousterian culture stage, by Breuil. The remains as finally described by Gorjanovic-Kramberger⁸² include hundreds of human bones intermingled in various separate strata with hundreds of stone implements and chips and thousands of animal bones. Of the contemporary fauna are recorded *Ursus spelæus*, *Bos primigenius*, *Equus ? caballus*, *Dicerorhinus merckii*, *Megaceros euryceros*, *Castor fiber*, *Arctomys marmotta*. The human racial type is unquestionably related to that found at Neanderthal and Spy. The race is somewhat dwarfed, of broader head form, with less prominent supraorbital processes. The species is *Homo neanderthalensis*.

Mousterian Culture, Temperate Fauna.—The earliest strata of the Mousterian culture stage in France show a fauna not differing essentially from that of the late Acheulean stage, namely, a fauna containing *Elephas antiquus* and *Dicerorhinus merckii*. Thus in La Micoque, one of the oldest stations in the Vézère valley, Dordogne, in which the culture belongs to the transition between late Acheulean and early Mousterian times, in the very lowest layers are found traces of the broad-nosed rhinoceros (*D. merckii*) associated with remains of the moose (*Alces*). But the last glacial stage is approaching and *D. merckii* gives place to the migrants from the tundra region of the northeast, covered with hair, adapted to an arctic climate, namely, the mammoth and the woolly rhinoceros. The main succeeding portion of the Mousterian culture was contemporaneous with the Fourth Glacial Stage and the cold tundra, steppe fauna.

⁸² GORJANOVIC-KRAMBERGER, KARL: "Der Diluviale Mensch von Krapina in Kroatien Ein Beitrag zur Paläoanthropologie. Studien über die Entwicklungsmechanik des Primatenskelettes mit besonderer Berücksichtigung der Anthropologie und Descendenzlehre." Herausgegeben von Dr. Otto Walkhoff. C. W. Kreidel's Verlag. 4to. Wiesbaden, 1906.

FOURTH GLACIAL STAGE—WÜRM, MECKLENBURGIAN, WISCONSIN

BEGINNING OF THE REINDEER AND CAVE PERIOD

The Fourth Glacial Stage, like the First, is believed to have been nearly contemporaneous in Europe and North America, consequently the estimates of Postglacial time in one country have an important bearing on the other. The First Maximum of the Fourth or *Würm* glaciation in the Alps is estimated by Penck as occurring 40,000 years ago. It was followed by the slight recession known as the *Laufenschwänkung*, a temperate retreat followed in turn by the Second *Würm* Maximum, which is estimated as occurring 20,000 years ago. Similarly in America the "early Wisconsin" is followed by a recession interval (*Peorian*), and this in turn by the "late Wisconsin" which is the final great glaciation in America. The contemporaneous *Mecklenburgian* of the North German lowlands gave rise to the "Upper Drift," which in some respects bears a striking resemblance to the Wisconsin Drift of America both in its systems of moraines and in its topography. This stage also includes apparently the "Upper Drift" of northern England with which the drift of the Alps correlates well. The Upper Drift of England covered also a large part of Wales. In Germany glaciation also occurred in the *Riesengebirge* and the Black Forest.

In America part of the "Upper Drift" is loess-covered and in the opinion of Koken and Schmidt the Upper Drift of Germany is also partly covered with the "Newer Loess." The Postglacial Stage did not exhibit a steady amelioration of climate after the culmination of the Fourth Glacial Stage, but there is evidence of great oscillations and renewed glacial advances both in northern Britain and Scandinavia and in Germany. These Postglacial advances, as most clearly defined in the Alpine region, have been termed by Penck the *Bühl*, the *Gschnitz* and the *Dau*n. They are correlated by palæontologists and anthropologists quite closely with the successive faunæ and archæological implements of Postglacial time.

Period of the Final Glacial Maximum.—The length of time which has elapsed since the close of the Fourth great glacial advance is estimated in America by the recession of the Falls of Niagara. This recession began with the end of the Wisconsin glaciation which is believed to have been contemporaneous with the *Würm*. As early as 1829 Bakewell estimated that since the Falls of Niagara were receding by the erosion of the Niagara gorge at the rate of three feet annually about 10,000 years had elapsed since the end of the Glacial Epoch. Lyell visited Niagara in 1841 and after consideration of all the data of erosion concluded that

the time since the last great glacial stage was not less than 31,000 years. Gilbert, Upham and other geologists of the United States Geological Survey after pointing out many sources of error in all such calculations were inclined to the adoption of periods ranging from 6,000 to 10,000 years. Gilbert's survey is the most careful which has been made; he estimated (1896) that the gorge of Niagara is not more than 7,000 years of age. The Canadian geologist Spencer arrived at a result almost identical with that of Lyell, namely, 32,000 years.

The most careful estimates on the subdivisions of Postglacial time in Europe are those of Penck (1909, p. 1168) which may be briefly summarized as follows:

IV. 2nd Würm Maximum, beginning of Upper Palæolithic culture.....	20,000 to 34,000 years
Achen retreat, period of Aurignacian and Solutrean culture	
Bühl advance, period of early Magdalenian culture (Neüsch)	16,000 " 24,000 "
Post-Bühl, period of late Magdalenian culture.....	10,000 " 16,000 "
Daun Stage, period of the close of the Upper Palæolithic, Azilian culture.....	7,000 "
Age of Copper in Europe.....	4,000 " 5,000 "

According to Heim's⁸⁰ calculations the period since the deposition of the Bühl moraines in the Lake of Lucerne amounts approximately to 16,000 years and if the Magdalenian culture deposits of this formation are of the age of the Bühl advance we may estimate with Neüsch that the Bühl advance occurred at least 24,000 years ago. This advance is a very important period because it represents the last of the Arctic, Tundra and Steppe Faunas in central Europe prior to the establishment of the modern forested conditions and fauna.

Fauna of the Fourth Glacial Stage.—The severe climate of the Fourth Glacial Stage is indicated by the mammalian life found at Achenheim and Sirgenstein associated with what is known as the "full Monsterial" Palæolithic culture (Schmidt, 1912). Here for the first time there is a predominance of the Tundra Fauna (fifteen species) as well as the advent of the Steppe Fauna (two species), while the Forest Fauna (seven species) and Meadow Fauna (four species) are still represented. The straight-tusked elephant (*E. antiquus*) and broad-nosed rhinoceros (*D. merckii*) have disappeared and are now replaced by the woolly elephant (*E. primigenius*) and woolly rhinoceros (*D. antiquitatis*). The mam-

⁸⁰ HEIM, A.: "Über das absolute Alter der Eiszeit." Vierteljahrsschrift der naturforsch. Ges. in Zürich, Jahrg. 39, No. 2, pp. 180-186. 1894.

mal life of the Fourth Glacial Stage at Achenheim and Sirgenstein near the upper Rhine is divided among the various faunæ as follows:

TUNDRA

Elephas primigenius
Diceros antiquitatis
Rangifer tarandus
Vulpes lagopus
Lepus variabilis
Myodes torquatus

STEPPE

Equus germanicus (Steppe type)
Spermophilus rufescens

FOREST

Cervus elaphus
Lynx lynx
Canis lupus
Vulpes alopec
Arvicola amphibius
Ursus spelæus

ALPINE

Arctomys marmotta
Ibex sp.?
Lagopus alpinus

MEADOW

Bison priscus
Bos primigenius

ASIATIC

Hyæna spelæa
Felis leo spelæa

This "Lower Rodent" stratum with a fauna such as we find at present in far northern Russia registers the coldest climate of Pleistocene times, corresponding to the Second Maximum of the Fourth Glacial Stage. It is well known that this Lower Rodent fauna is not local but rather a widespread phenomenon extending over northern and southern Germany and Belgium (Schmidt, 1912, p. 261). The presence of this Lower Rodent fauna at Thiede near Braunschweig in the border region of the Upper Glacial Drift of Germany is of special significance, as Wahnschaffe observes. This is the classical locality for lemming, the remains of lemmings being associated solely with those of arctic fox, arctic hare, reindeer, musk ox and mammoth.

After the First Maximum of the Fourth glaciation the Laufenschwänkung may have temporarily favored the return of the *Elephas antiquus* and *D. merckii* fauna as far as northern France because we occasionally find a glacial mixed fauna where *E. antiquus* and *D. merckii* occur in association with *E. primigenius*. The close of the Fourth Glacial Stage or Second Würm Maximum is marked by the first appearance of very numerous arctic rodents, especially of the banded lemming (*Myodes torquatus*) type, which constitute the so-called "Lower Rodent" layer. The animals (Schmidt, 1912) characteristic of this Lower Rodent stratum as found at Sirgenstein, Wildscheuer and Ofnet are as follows:

TUNDRA

Canis lagopus
Fætorius erminea
Lepus variabilis
Myodes obensis
 " *torquatus*
Lagopus albus

FOREST

Arvicola amphibius

MEADOW

Talpa europæa

Upper Sands of Mauer.—In the Upper Sands of Mauer, Wurm (*op. cit.* 1913) and Förster⁸⁴ have observed the presence of a sub-Arctic cold fauna including the arctic reindeer (*R. tarandus*) and the banded lemming (*Myodes torquatus*), the steppe suslik (*Spermophilus rufescens*), also the steppe weasel (*Fætorius eversmanni*). This is positively correlated with the fourth glaciation by Wurm.

The fauna of the Wildkirchli cave on Mont Centis in Switzerland shows no typical interglacial forms and may indicate either the approach of the Würm Glacial period or its Laufenschwängung (Schmidt, 1912, p. 193).

Mousterian Palæolithic Culture.—The Mousterian Palæolithic culture of the Neanderthaloid race appears to have begun toward the close of the Third Interglacial Stage and continued throughout the entire period of the Fourth Glacial, including the First Maximum, the Laufenschwängung, and the Second Maximum, ending with the "Lower Rodent" fauna in the deposits of the "Newer Loess." Thus Koken and Schmidt speak of the Mousterian culture as found at the base of the "Younger Loess."

The early men of the Mousterian culture period witnessed in the north the *Elephas antiquus* and broad-nosed rhinoceros, and the hippopotamus in the south, as proven in the Prince's Cave of Monaco. The culture lasted through all the severe climatic conditions of the entire Fourth Glacial Stage. The men of the Neanderthal race in Mousterian times sought the rock shelters and grottos or entrances to caverns so that the greater number of palæoliths are found mingled with the remains of animals of the chase around the old hearths. The commonest game evidently consisted of the wild horse, urus and reindeer. Less frequently the ibex and stag were objects of the chase.

Neanderthal Races.—To the Neanderthal race (*Homo neanderthalensis*,⁸⁵) in addition to the remains of Krapina, belong many and widely distributed remains, including the classic type of Neanderthal discovered in 1856, the Gibraltar skull discovered in 1848, those of La Naulette, Spy (1887), Krapina (1902), Malarnaud, La Quina, Le Moustier (1908) and La Ferrassie. The skull of Neanderthal man was character-

⁸⁴ FÖRSTER, F.: "Über eine diluviale subarktische Steppenfauna aus den Sandhügeln von Mauer." Verhandl. naturw. Verein. Karlsruhe, 1913.

⁸⁵ The mid-Pleistocene man was definitely named *Homo neanderthalensis* by Cope in 1893 at the time of the discovery of the skeletons of Spy; it seems, however, that King had previously (1864) used the same term. Schwalbe (1901) remarks, . . . "the species of man which I, together with King (1864) and Cope (1893), designated as *Homo neanderthalensis*." In the following year (1902) the same author introduces the term *Homo primigenius*, which is that generally adopted in Germany. Among French authors the same man is known to-day as *Homo mousteriensis*. This polynomial usage serves at least to emphasize the unanimous opinion as to the distinct specific character of mid-Pleistocene man.

ized by an extremely receding forehead, by the great prominence of the supraorbital ridges, and by a rather slender jaw. The occipital projection for the attachment of the superior muscles of the neck was large, indicating that these muscles at the back of the neck were strongly developed, a character necessary to meat-eaters before the invention of knives

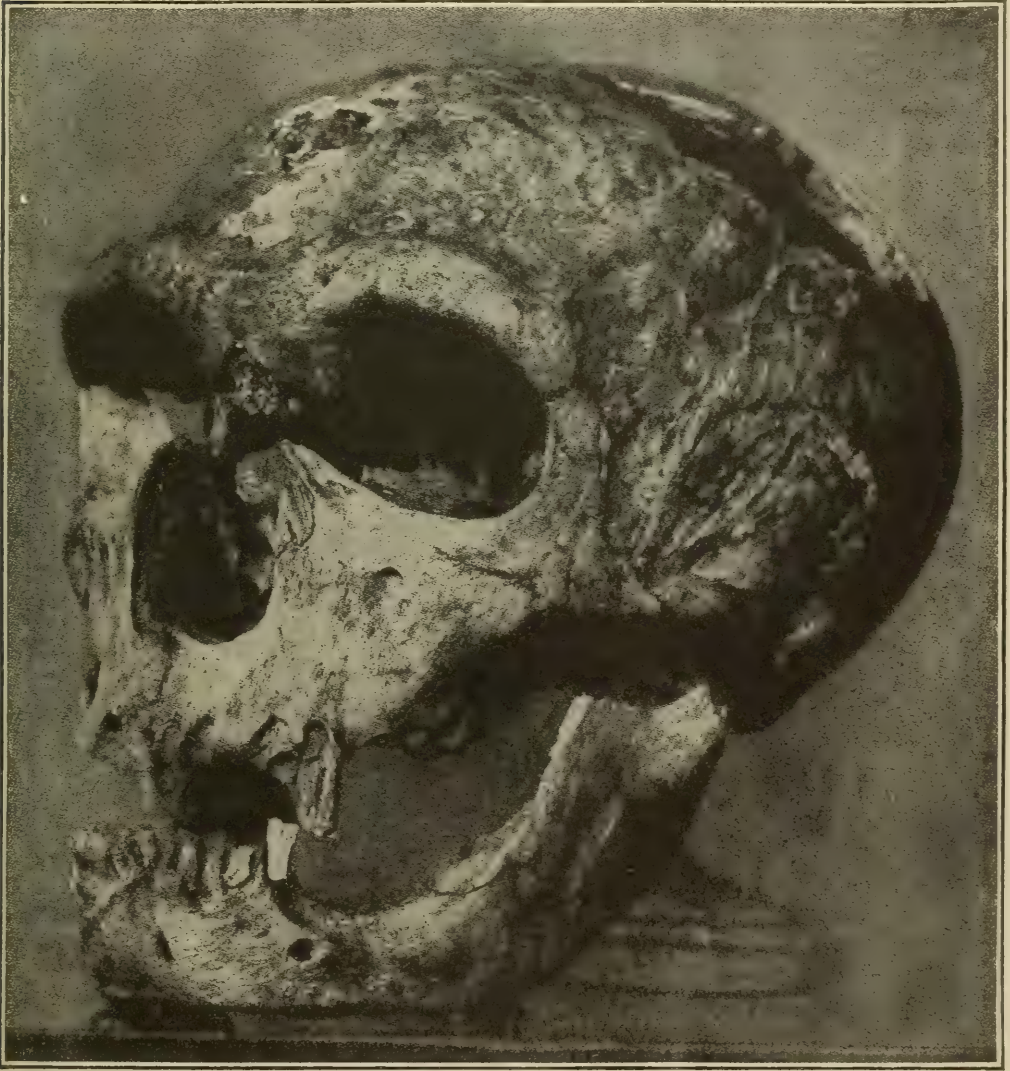


FIG. 16.—*Neanderthal skull*

Skull of a Neanderthal man from the cavern of La Chapelle-aux-Saints (Corrèze), France.
After Boule.

and forks. This primitive type of man was shorter than the average European (that is, 5 feet 8½ inches); he is estimated of as low stature as 5 feet 3½ inches. His lower limbs were especially powerful, but his gait seems not to have been fully erect, for the knees are bent slightly forward.

The most remarkable skull and skeleton of Mousterian age is that (Fig. 16) found by the Abbés J. and A. Bouyssonie and L. Bardon in the cavern of La Chapelle-aux-Saints (Corrèze) in 1908, associated with stone implements and remains of the reindeer, urus, ibex and woolly rhinoceros. The cranium is dolichocephalic, with prominent supra-



FIG. 17.—*Neanderthal man*

Reconstruction of the head of *Homo neanderthalensis* by Charles R. Knight under the direction of the author. 1910.

orbital processes and relatively short and broad nose, weak lower jaw, lacking the prominent chin process. These characters, as well as the posterior position of the foramen magnum and the form of the palate, are distinctly simian or pro-human.⁸⁶

POSTGLACIAL STAGE—CONTINUATION OF UPPER PALEOLITHIC, REINDEER OR CAVE PERIOD

CLIMATE

For a long period the fauna of Postglacial time in Europe remained practically the same, namely, during the Mousterian, Aurignacian, Solutrean and Magdalenian culture periods. The cold fauna is shown both in the animal remains and in the art, which is so characteristic of Aurignacian and Magdalenian times.

As the "Lower Rodent" layer of Mousterian times is referred to the Second Maximum of the Fourth glaciation and the period of most intense

⁸⁶ BOULE, M.: "L'Homme Fossile de la Chapelle-aux-Saints." *L'Anthropol.* Vol. XIX, pp. 519-525. 1909.

cold it is followed by an amelioration of climate (Achenschwänkung) during Aurignacian and Solutrean times, which in turn is succeeded by a recurrence of a colder climate during the Bühl advance, at which stage it is believed the "Upper Rodent" layer of Magdalenian times indicates a fresh invasion of Arctic-Tundra types. This tundra "Upper Rodent" layer occurs in the deposits of Sirgenstein, Wildsheuer and Ofnet; it is associated along the upper valley of the Danube with early Magdalenian palæoliths, and continues in Hohlefelds, Schussenquelle, Andernach, Münzingen and Wildscheuer in association with the Middle Magdalenian culture stage; there is, moreover, in Hohlefelds, Schmiechenfels and Propstfelds an association of the cold steppe fauna with a late Magdalenian culture stage. After this there was a decided amelioration of climate, for in the final Azilian-Tardenoisian stage all the Steppe, Tundra and Alpine types disappear.

UPPER PALÆOLITHIC, FOUR OR FIVE HUMAN RACES

(1) The *Grimaldi* Race, a negroid type is found close to the warm faunal level at Mentone. (2) An initial feature of the long Postglacial Stage is the entire disappearance of the Neanderthal race of men and the invasion of Europe by a new race of the much higher *Crô-Magnon* type referred to the existing human species (*Homo sapiens*). This race was discovered in Dordogne at the hamlet of Crô-Magnon from which it takes its name. It has also been found in the caverns near Mentone lying above remains of the Grimaldi race. Crô-Magnon remains are also found at several localities in France in deposits of Aurignacian and Magdalenian times. In the south in Aurignacian times this was a tall, well-proportioned, hunting and nomadic race; in the more severe climate of the north it occurs as a dwarfed race. The skulls are dolichocephalic, with very broad cheek bones, hence designated as *disharmonic*. The brain capacity is equal to that of the early Neolithic races and surpasses that of many modern races. It is probable but not positively demonstrated that to this Crô-Magnon race we owe the early arts of engraving, sculpture, design and mural painting which are preserved in the Aurignacian and Magdalenian deposits of France and northern Spain. (3) In Solutrean times there was at Brünn and Předměst (Moravia) another dolichocephalic race which is considered as distinct or transitional because unlike the typical Crô-Magnon race the cheek bones are narrow and the skull is thus *harmonic*. This is the *Brünn-Předměst* race. (4) After the close of the Magdalenian culture stage, or during the so-called Azilian-Tardenoisian culture, the first brachycephalic human races make their appearance in Europe. Their remains have been

found at Ofnet, Furfooz and at Grenelle. This is commonly known as the *Grenelle* or *Furfooz* race; it is very distinct from the preceding races in bodily structure and in culture.

Aurignacian, First Upper Palæolithic Culture Stage.—This first of the Upper Palæolithic culture stages is widely distributed in western Europe. It takes its name from the small grotto of Aurignac (Haute Garonne) where the first discoveries of the culture and of a number of skeletons were made in 1852. The arts of engraving on bone and stone, of drawing and painting in single lines, of sculpture of the human and of animal figures, all in bold but primitive forms, first appear in Aurignacian times. Thus man through his art begins to make a permanent record of the contemporary mammalian life, especially of the mammoth, bison, reindeer and cave bear. With early Aurignacian times the cold climax is passed but we still find remains of the Arctic lemming (*Myodes torquatus*) fauna. The mammalian list of the Aurignacian stations both of the "Newer Loess" and of the caverns still gives a cold aspect with its Tundra-Steppe-Alpine types with which no warmer types are associated. In middle and late Aurignacian times the lemmings for a time disappear; otherwise the fauna retains its northern character (*Gulo luscus*, *Lagopus alpinus*), which is not essentially altered by the presence of the hyæna and stag.

Solutrean, Second Culture Stage.—This stage, which takes its name from the type station of Solutré (Saône-et-Loire) represents the climax of perfection in the Upper Palæolithic flint industry, which appears to represent partly a development of Aurignacian workmanship and partly a culture invasion. With Solutrean times Schmidt correlates the three Brünn skeletons and Předměstí (Moravia). It is noteworthy that no evidences of a Solutrean art have been discovered. The fauna like that of the Aurignacian represents an amelioration of the extreme cold of the Fourth Glacial maximum. The wild horse and reindeer are abundant as well as the mammoth, rhinoceros, wolf and cave bear. Perhaps the somewhat more frequent appearance of such cold faunal types as the Alpine hare and grouse betoken the approach of the colder Bühl stage of Magdalenian times.

Magdalenian, Third Culture Stage and Fauna.—This third Upper Palæolithic culture takes its name from the station of La Madeleine (Dordogne). It is distinguished by decline in the perfection of the flint industry as compared with the Solutrean stage, by a very decided development of bone implements, and by a surprising advance in the arts of engraving and painting and the sculpture of animal forms in bone and ivory. The Magdalenian stage corresponds with the "Upper Rodent"

strata which registers a period of extreme cold correlated with the Bühl glaciation (Penck, Schmidt), which again attracts the cold-loving rodents. The "Upper Rodent" strata associated with Magdalenian cultures in the shelters of Schweizersbild and Kesslerloch are of more recent date than the neighboring "Lower Terraces." This "Upper Rodent" stratum contains an abundance of Tundra and Steppe types of smaller rodents and represents the last stage of extreme cold in Europe. Thus the banded lemming (*Myodes torquatus*) corresponds with early Magdalenian times. In the upper levels of the Upper Rodent layer, which belong to late Magdalenian times, the Tundra fauna gradually gives way to a more abundant Steppe fauna, the banded lemmings becoming less frequent while the jerboas (*Alactaga jaculus*), the hamsters (*Cricetus phæus*), the susliks (*Spermophilus rufescens*) become more abundant. The reindeer and the wild horse are very abundant. The mammoth, the woolly rhinoceros and the cave bear gradually retire from the middle and southern mountains of Germany, and in the very highest Magdalenian culture layers the fauna begins to approach that of recent times, namely, the Eurasiatic Forest fauna. In Schmidt's opinion there is no question as to the similarity of age of the Magdalenian layers of the Münzingen loess deposits with the cave deposits of Schweizersbild and Thaingen. From this evidence it can be positively determined that the chief deposits of the "Newer Loess" occurred after the Fourth glaciation.

With Magdalenian times are associated the skeletons of La Madeleine, Laugerie Basse, Chancelade, La Hôteaux and Duruthy; all are regarded as of the Crô-Magnon racial type.

POSTGLACIAL FAUNA

The mammal fauna of this long Postglacial period is the same in the upper valleys of the Rhine, the Danube, the Dordogne and the Garonne. It extends throughout the Pyrenees and the Cantabrian Alps of northern Spain. Even the reindeer invaded this region (Harlé) but the stag (*C. elaphus*) is more abundant. The moose (*Alces*) also invaded the Pyrenees and northern Spain. The Saiga antelope (*S. tartarica*) occurs at thirteen localities in southern France (Harlé), and the steppe suslik (*S. rufescens*) is very abundant.

It is a grand assemblage of the European Forest and Meadow types mingled with a few Eurasiatic-Alpine types, abundant Eurasiatic Forest types, but with the Tundra and Steppe types predominating numerically until the close of the Magdalenian period, when the Forest types again begin to greatly predominate. The numerical succession in Germany and Austria may be tabulated from the invaluable tables presented by

Schmidt. We owe our knowledge of the cold fauna of southern France chiefly to Harlé (1871-1912).

	Tundra species	Steppe species	Alpine species	Meadow species	Forest species
Postglacial, Daun Stage, Azilian-Tardenoisian Culture, Ofnet, Istein.....	7
Postglacial, Gschnitz Stage, Hohlefelds. Late Magdalenian Culture.....	7	6	1	5	12
Postglacial, Middle Magdalenian Culture, Upper Rodent Strata.....	10	7	..	6	8
Postglacial, Early Magdalenian Culture, Bühl Stage, Sirgenstein.....	9	5	..	5	3
Postglacial, High Magdalenian Culture, Thaingen.	15	14	4	13	21
Postglacial, High Magdalenian Culture, Schweißersbild	7	2	2	6	8
Postglacial, Solutrean Culture.....	6	3	..	2	2
Postglacial, Late Aurignacian Culture.....	10	4	1	1	5
Postglacial, Aurignacian Culture, Sirgenstein, Ofnet	7	1	1	1	3
IV. Glacial Maximum, Lower Rodent Layer.....	7	4	..	2	3
IV. Glacial Stage, Mousterian Culture.....	8	5	1	2	4

The fauna of Vöklinshofen includes a similar intermingling of tundra, steppe, mountain, and meadow-forest types. The same is true of the scattered deposits⁸⁷ in Thuringia near Saalfeld, Gera, Jena, Leipzig, etc. The loess fauna near Würzburg, Bavaria,⁸⁸ also includes twenty species of mammals divided into typically modern tundra forms of northern Asia, typical modern steppe forms of central Asia and Siberia, together with the four characteristic great mammals of the period, the mammoth, the woolly rhinoceros, urus and bison. The arctic character of the fauna of Châteauneuf-sur-Charente⁸⁹ in central France is very conspicuous, most of the species belonging either to the tundras or the steppes of modern Europe. The bones of many young animals occur in this deposit, which may be explained perhaps on the supposition that the animals fell into the fissure while the opening was lightly covered with snow, the young being the most frequently entrapped. Among the chief localities where this grand Fourth Glacial and Postglacial fauna have been discovered are the following:

⁸⁷ POHLIG, H.: "Vorläufige Mittheilungen über das Plistocæn, insbesondere Thüringens," Sitzungsber. Niederrhein. Ges. Bonn, pp. 2-15. Mar. 3, 1884.

⁸⁸ NEHRING, A.: "Übersicht über vierundzwanzig mitteleuropäische Quartär-Faunen," Zeitschr. deutsch. geol. Ges., pp. 468-509. Jahrg. 1880.

⁸⁹ BOULE, M., and CHAUVET, G.: "Sur l'existence d'une faune d'animaux arctiques dans la Charente à l'époque quaternaire," C. R. Acad. Sci. Paris, Vol. XXVIII, pp. 1188-1190. 1899.

Localities

KESSLERLOCH Cave, near Thaingen (Fig. 9, 37)
 SCHWEIZERSBILD Cave, near Schaffhausen (37)
 Scattered deposits in Thuringia, in northern Germany.
 Saalfeld, Gera, Jena, Leipzig (29, 30, 31)
 WÜRZBURG, Bavaria, Loess deposits (33)
 SWABIA and FRANCONIA, cave deposits
 VÖKLINSHOFEN, Alsace (28)

Culture Zones

Magdalenian Stage
 Magdalenian Stage
 Aurignacian and Solutrean Stages
 Solutrean Stage
 Aurignacian and Solutrean Stages
 Magdalenian Stage
 CHÂTEAUNEUF-SUR-CHARENTE (Charente) (36)

The large mammals of the period are more fully known than in any previous Pleistocene stage both through palæontological researches, which date back to the beginnings of the science of vertebrate palæontology in Germany and France, and through the extraordinarily accurate carvings and drawings in the caverns of Dordogne and northern Spain. These drawings have been reproduced with remarkable fidelity, chiefly by Breuil.⁹⁰ The chief elements in the larger mammal fauna were as follows:

FOREST AND MEADOW FAUNA

Moose, *Alces palmatus*
 Persian deer, *Cervus maral*
 Red deer, *Capreolus capreolus*
 Roedeer, *Cervus elaphus*
 Wild cattle, *Bos primigenius*
 Bison, *Bison priscus*
 Forest horse, *Equus caballus*
 Bear, *Ursus spelæus*
 Lion, *Felis leo spelæa*
 Brown bear, *Ursus arctos*
 Wild boar, *Sus scrofa*

TUNDRA FAUNA

Woolly rhinoceros, *Diceros antiquitatis*
 Woolly elephant, *Elephas primigenius*
 Musk ox, *Ovibos moschatus*
 Reindeer, *Rangifer tarandus*
 Arctic fox, *Vulpes lagopus*
 Elasmotherium, *Elasmotherium sibiricum*

Schweizersbild Cave (Fig. 9, 37).—The Magdalenian, or reindeer man apparently arrived in the Schaffhausen region long after the maximum Fourth glaciation, during the Bühl advance, the period of deposition of the "Upper Rodent" layer with its cold Arctic and Steppe fauna. The deposits of the Schweizersbild cave as recorded by Nehring⁹¹ present the fullest succession and extend over a very long period of time as exhibited in the following layers:

Neolithic:

5. Gray culture layer, forest fauna.

⁹⁰ See publications of Abbé Henri Breuil, Marcellin Boule, Le Comte Begouen, P. Bourrinet, L. Capitan, Emile Cartailhac, Lalanne, Lartet and Christy, Déchelette, Hugo Obermaier, Pèyrony, Reinach. Others are in preparation.

⁹¹ NEHRING, A.: "Übersicht über vierundzwanzig mitteleuropäische Quartär-Faunen." Zeitschr. Deutsch. Geol. Ges., pp. 468-509. 1880.

—: "Die kleineren Wirbeltiere vom Schweizersbild bei Schaffhausen." Denkschr. allg. schweiz. Ges. gesäm. Naturwiss., Vol. xxxv, pp. 41-77. 1896.

STEPPE FAUNA

Saiga antelope, *Antelope saiga*
 Asiatic wild ass, *Equus hemionus*
 Wild horse, *E. przewalskii* ? sp.
 Jerboa, *Alactaga jaculus*
 Desert horse, *E. caballus celticus*

ALPINE FAUNA

Ibex, *Ibex priscus*
 Chamois, *Rupicapra*

Palæolithic, Magdalenian:

4. Upper Breccia, or "Upper Rodent" layer, steppe fauna.
3. Yellow culture layer, palæolithic "Reindeer Age," steppe fauna.
2. Lower Breccia, or "Lower Rodent" layer, animal remains and traces of man, tundra fauna.
1. Diluvial layer. No fossils.

(2) Of these the "Lower Rodent" layer contains a pure arctic tundra fauna, such as the vole, hare, fox, the reindeer, the ptarmigan. There are no traces of man. In the layer above these the early steppe animals begin to appear, the hamsters and picas. (3) Then in the "Yellow Culture" layer there is an assemblage of pure steppe forms, susliks, dwarf picas and wild horses, all pointing to the absence of forests; but at the top of this layer the first squirrel (*Sciurus*) appears as the harbinger of forests. (4) In the "Upper Rodent" layer the steppe fauna begins to be intermingled with an increasing number of forest types, such as squirrels, dormice, and the pine marten. (5) Finally we reach the "Gray Culture" layer, composed of the modern forest dwellers, such as the squirrel, the beaver, the pine marten, the stag, the roe, the wild boar, the brown bear. The "Lower Rodent" layer is contemporaneous with the Mousterian culture, while the "Upper Rodent" layer belongs to Magdalenian times. The uppermost "Gray Culture" layer with its forest fauna belongs either to the closing Palæolithic or to Neolithic times.

Kesslerloch Cave.—Similar conclusions result from the study of the geologic conditions surrounding the Kesslerloch Cave of Thainingen in Switzerland (Fig. 9, 3†). This famous cave lies on the edge of a moderately wide valley, traversed by a brook.⁹² In this sheltered, well-watered, hilly region, woods flourished and harbored the forest animals, at the same time that the glaciers retreating southward left damp and stony areas, closely followed by a tundra fauna. The woolly rhinoceros and the mammoth persisted longer here than in other parts of Europe. As analyzed by Nüesch, we discover here mammals distinctive of the tundras, of the steppes, of the modern Alps (marmot, chamois, ibex), of the meadow-forests (bison, urus), and finally of the modern forest type (lion, wolf, brown bear, pine marten, squirrel, wild boar, and stag). These mammal zones undoubtedly correspond with the passing or evolution of

⁹² NÜESCH, J.: "Das Kesslerloch, eine Höhle aus paläolithischer Zeit. Neue Grabungen und Funde." Neue Denkschr. allg. schweiz. Ges. gesam. Naturwiss., Vol. XXXIX, Pt. 2, pp. 1-72. 1904.

several human culture stages (perhaps the Aurignacian, Solutrian, and Magdalenian). While the tundra fauna was pushing southward into the heart of Switzerland, it had already vanished from central Germany, Belgium and France, where it had been superseded by a steppe, or even a meadow-forest fauna. The human artifacts show that these deposits are contemporaneous with those of Schweizersbild, both belonging to Magdalenian times. A hearth, with ashes and coals, and many charred bones of old and young mammals, including the woolly rhinoceros, have been found here. The human remains show that a race of pigmies dwelt here smaller even than the small men of Schweizersbild, their height being estimated at 120cm. (4 feet).⁹³ The horse of Kesslerloch shows many resemblances to the Przewalsky horse of the high steppes of Central Asia.⁹⁴

It is characteristic of these faunas that among species still living are mingled remains of the great extinct mammals of the times. Another feature is that occasionally the Steppe, Tundra and Forest faunas are found either nearly pure or entirely distinct and separate as in the lower deposits of Thiede near Braunschweig, above cited. More often as in Schweizersbild and Kesslerloch they are successive or superposed upon each other.

Beside the cavern deposits are those in the loess. Thus in the "Upper Loess" near Würzburg, Bavaria, Nehring⁹⁵ has recorded both a Tundra and a Steppe fauna, including beside the still living types the woolly rhinoceros, the mammoth, the urus and the bison.

MIGRATIONS OF THE LARGE MAMMALS OF THE FOURTH GLACIAL AND POSTGLACIAL PERIOD

Over the greater part of the Iberian Peninsula the stag (*Cervus elaphus*) took the place of the reindeer. There is no trace of the entrance of the Steppe Fauna at any period into Spain or Portugal. The Pyrenees also presented a barrier to the greater part of the tundra fauna, yet the Norwegian lemming (*Myodes lemmus*) penetrated Portugal to the vicinity of Lisbon. The cold fauna (*E. primigenius*, *E. antiquitatis*, *U. spelæus*, *F. spelæa*) is not represented in Portugal, but *E. primigenius* has been discovered in two localities on the extreme northern coast of Spain, in the Province of Santander bordering the Bay of Biscay. *D. antiquitatis* also occurs in the same province.

⁹³ NÜESCH: *op. cit.*, p. 21.

⁹⁴ STUDER, T.: "Die Knochenreste aus der Höhle zum Kesslerloch bei Thayngen," *Neue Denkschr. allg. schweiz. Ges. gesam. Naturwiss.*, Vol. XXXIX, Pt. 2, pp. 73-112. 1904.

⁹⁵ NEHRING, A.: "Übersicht über vierundzwanzig mitteleuropäische Quartär-Faunen," *Zeitschr. Deutsch. Geol. Ges.*, pp. 468-509. 1880.

Rangifer tarandus is found in the cavern of Serinya south of the Pyrenees (Torrallba). It also has been recorded recently (Obermaier) in the cavern of Altamira, near Santander. The Alpine chamois (*Rupicapra*) occurs south of the Pyrenees and the ibex is traced to Gibraltar.

Thus Harlé⁹⁶ concludes it is certain that the "cold fauna" of France spread along the northern coast of Spain flanking the Pyrenees into Catalonia, including the mammoth, reindeer, chamois, woolly rhinoceros, and spreading as far west as Santander. This is also the range of the Crô-Magnon race of men.

Mammoth.—The woolly mammoth (*E. primigenius*) now reaches the height of its evolution and specialization. As preserved in the frozen tundras of northern Siberia and as represented in very numerous drawings and engravings by the Upper Palæolithic artists, it is the most completely known of all fossil mammalia. Its proportions as shown in the accompanying figure, which represents the information gathered from all sources, are entirely different from those of either the Indian or African elephant. The head is very high and surmounted by a great mass of hair and wool. Behind this is a sharp depression separating the back of the head from the great dorsal hump. The hinder portion of the back falls away very rapidly and the tail is short. The overcoat of long hair nearly reaches the ground, and beneath this is a warm undercoating of wool.

As described by Salensky⁹⁷ from the wonderfully complete specimen discovered in 1901 on the banks of the Beresowka River in northeastern Siberia, this animal developed characters which absolutely exclude the possibility of its ancestry or relationship to the existing Indian elephants. The hind foot was four-toed, or tetradactyl, and not five-toed as in the living forms. The head was larger as compared with the length of the body than in recent elephants, a character which stands in close connection with the enormous development of the tusks; these were distinguished by their spiral form, the points directed inward. The ears were very small and covered with hair. The tail was relatively shorter than in the existing elephants and was provided with a tassel of long, bristly hair at the end. The color of the hair was yellowish brown, varying from light brown to pure brown, and a coat of woolly hair, 2 to 2½ cm. in length, covered the whole body. Interspersed with these were a large number of longer and thicker hairs which formed mane-like patches on

⁹⁶ HARLÉ, EDOUARD: "Les Mammifères et oiseaux quaternaires connus jusqu'ici en Portugal. Memoire suivi d'une liste générale de ceux de la Péninsule Ibérique." Commun. du Service Géol. du Portugal, Tom. viii. pp. 22-85. pll. I-V. Lisbon, 1910.

⁹⁷ SALENSKY, W.: Über die Hauptresultate der Erforschung des im Jahre 1901 am Ufer der Beresowka entdeckten männlichen Mammutcadavers." C. R. Séa. Six. Congr. Internat. Zoöl., pp. 67-86. Berne, 1904.

the cheeks, on the chin, on the shoulders, flanks, abdomen, etc. A broad fringe of this long hair extended along the sides of the body as depicted in the palæolithic sketches from the Combaurelles Cave discovered by Capitan and Breuil in 1901. Especially interesting is the food found in the stomach and mouth, which consists of a meadow flora such as characterizes this region of Siberia at the present day, thus appearing to disprove the theory that the climate was milder than that now prevailing. Nor does it appear that it was more frigid, because there are few repre-



FIG. 18.—The hairy mammoth (*Elephas primigenius*) and Palæolithic man (*Homo neanderthalensis*)

Restored by Charles R. Knight under the direction of the author, 1914. Original in the American Museum of Natural History, New York City.

sentatives of tundra vegetation. Grasses (*Gramineæ*) and sedges (*Cyperaceæ*) predominate. There were also wild thyme (*Thymus*), beans of the wild oxytropis (*Oxytropis compestris*), seeds of the alpine poppy (*Papaver*), and the boreal variety of the upright crowfoot (*Ranunculus acer*), all still found in this region.

Woolly Rhinoceros.—The woolly rhinoceros (*D. antiquitatis*, *D. tichorhinus*) is distinctly a cold-weather, or tundra form and the invariable companion of the mammoth. Like *D. merckii* it has no front, or cutting teeth hence it has been improperly considered as related to this species, but it really belongs to the modern African group of *Diceros* (*Ate-*

lodus), which is distinguished by a very elongate front horn (Fig. 19) and a small posterior horn, as in the existing white rhinoceros (*D. simus*) of Africa. The resemblance of the cave drawings of the Pleistocene animal to the living form is very close indeed except as regards the heavy coat of hair, which, as in the mammoth, extends far below the body. The hair of the face, of a golden brown color with an under-covering of wool, is preserved in the St. Petersburg Museum. Through a discovery (1911) at Starunia⁹⁸ in East Galicia this animal is now



FIG. 19.—*The woolly rhinoceros (Diceros antiquitatis)*

Restored by Charles R. Knight under the direction of the author, 1914. Original in the American Museum of Natural History, New York City.

completely known to us except the tail. The remains of the woolly rhinoceros were found at a depth of 13.6m., including the head, the left fore leg and the skin of the left side of the body, all with the musculature but lacking the hair. The Starunia specimen exhibits a broad, truncated upper lip, small, oblique eyes, ears long, narrow and pointed, a long nasal horn with oval base and shorter frontal horn, a short neck,

⁹⁸ NIEZABITOWSKI, E. L.: "Die Überreste des in Starunia in einer Erdwachsgrube mit Haut und Weichteilen gefundenen *Rhinoceros antiquitatis* Blum. (*tichorhinus* Fisch.). Vorläufige Mitteilung." Bull. Acad. Sci. Cracovie, Ser. B, pp. 240-267. April, 1911.

on the back of which is a small hump quite independent of the skeleton. The larger hump on the shoulders is formed by the long vertebral spines. The legs are comparatively short. The skin is smooth. Niezabitowski observes that *D. antiquitatis* resembles *D. simus* most closely, having in common the elongate head with prominent orbits, the truncated upper lip, the hump on the neck, and the short legs: it differs from *D. simus* in the somewhat narrower muzzle, small, pointed ears and the presence of a thick coating of hair.



FIG. 20.—*Rhinoceros* skulls

Skulls of the Pleistocene "woolly rhinoceros," *Diceros antiquitatis* of Eurasia (above), and of the recent African "white rhinoceros," *Diceros simus* (below). In the American Museum of Natural History.

Like *D. simus*, *D. antiquitatis* was a plains dweller living on grass and small herbs. The woolly rhinoceros was confined more closely to the edges of the great ice sheets than the mammoth: that is, it did not migrate so far to the south, stopping at the Alps, while the mammoth wandered into Italy as far south as Rome.

Elasmotheres.—The elasmothere (*Elasmotherium sibericum*) was another companion of the mammoth which ranged over eastern Europe, Germany, and southern Siberia. It was probably a steppe dweller. In Pleistocene times it is reported as occurring as far south as Sicily.⁹⁹ It

⁹⁹ BRANDT, J. F.: "Mittheilungen über die Gattung *Elasmotherium*, besonders den Schädelbau derselben." Mem. Acad. Imper. Sci. Pétersbourg. Ser. VII. Vol. XXVI, No. 6. St. Petersburg. 1878. and GAUDRY and BOULE. "Matériaux pour l'Histoire des Temps Quaternaires." Fasc. 31. L'Elasmotherium. Paris, 1888.

is a gigantic animal, distinguished from all the European Pleistocene rhinoceroses by the entire absence of the anterior horn and the possession of an enormous horn situated on the forehead between the eyes; also by the elaborate foldings of its dental enamel, to which the name *Elasmotherium* refers. Its hypsodont and folded teeth were especially adapted to a grassy diet, and Gaudry connects its appearance in Europe with the extensive deforestation accompanying the Steppe and Tundra periods of mammalian life. It apparently wandered into Europe from central Asia and never became very abundant. The elasmothere is possibly descended¹⁰⁰ from the *Aceratherium* of the Upper Miocene of Eppelsheim which has perfectly smooth, pointed nasals, and the rudiment of a horn between the eyes.

Horses of the Pleistocene.—The horse was distributed all over the northern hemisphere in Pleistocene times in the Glacial, Interglacial, and Postglacial Epochs. In America no Postglacial horses are found. In Europe horses were apparently abundant in Postglacial times and two of the natural breeds appear to have given origin to two of the modern domesticated types. The horses of the long warm Second Interglacial Stage were remarkable for their great size (*E. süßenbornensis*, *E. moshbachensis*) which exceeded that of the largest recent breeds (Pohlig, 1907).¹⁰¹ According to Pohlig the horses were at all times accompanied by the wild asses (*E. hemionus*) but this we are inclined to believe was a special feature of the dry and cold steppe periods in which we should expect to find asses similar to the dzeggetai of Asia of present time. The existing wild ass, or kiang, of the Asiatic steppes certainly appears in early Postglacial times at Wildscheuer, Thaingen, Kesslerloch, and Schweizersbild associated with the late Aurignacian Palæolithic culture. Reference of the ancient Pleistocene horses to *E. caballus* is certainly erroneous. The connection of these ancient Pleistocene horses with the modern species and races requires further investigation.

We should expect to discover in Europe horses of three different habitats or life zones, namely, of the dry African-Asiatic plains, of the Eurasiatic forests and meadows, of the tundras and steppes. Such anticipation appears to be verified through the new lines of study instituted by Ewart¹⁰² since 1904. Following more or less closely the work of previous students of the Equidae he has shown that the different wild breeds of horses have evolved in three kinds of environment. Thus we discover

¹⁰⁰ OSGORN, H. F.: "Frontal Horn on *Aceratherium incisurum*. Relation of the type to *Elasmotherium*," Science, N. S., Vol. IX, No. 214, pp. 161-162. Feb., 1899.

¹⁰¹ POHLIG, H.: Eiszeit und Urgeschichte des Menschen. Leipzig, 1907.

¹⁰² EWART, J. COSSAR: "The Multiple Origin of Horses and Ponies." Trans. Highland Agric. Soc. of Scotland, pp. 1-39. 1904.

horses adapted to: (1) forests and upland valleys; (2) high, dry, cold steppes; (3) warm deserts and plateaus. In these three chief habitats the horses may be respectively known as the "forest horse," the "steppe horse," and the "desert horse." Each has its distinctive coloring, tooth structure, and proportions of the skull, body and limbs, in adaptation to its peculiar mode of life.

The forest horse is relatively a large, clumsy animal. The face is arched, as in the modern draught horse. The limbs are short, the front cannon bone (Mtc. III) being short and stout, the length only $5\frac{1}{2}$ times the width. The tail is depressed in contrast with that of the desert horse. According to Ewart this type of horse (*E. robustus*) occurs at Solutré and in the Neolithic deposits of Ilford (Essex), and Kent. In Aurignacean times Solutré was the site of a great open air Palæolithic camp. Toussaint enumerates fragments of at least 100,000 horses, which mingled with other bones of the chase formed a sort of rampart around the camp. The majority of these horses belonged to the stout-headed, short-limbed forest, or Norse type, measuring 54 inches (13.2 hands) at the withers, the size of the existing pony.¹⁰³ The large joints and hoofs were especially adapted to the low-lying marshy ground in the vicinity of forests, and the long teeth and powerful jaws were adapted to feeding during parts of the year on coarse grasses, roots and other hard substances. There is no evidence that the men of the Aurignacean age either bred or reared these animals. The majority of the remains are those of horses from five to seven years of age. This type of horse is engraved on the walls of the cave of Combarelle, where the drawings are chiefly of old Magdalenian age and the pure forest type of horse is most frequently represented. There is also a small, fine-headed type suggesting the desert horse, and a larger, long-armed type suggesting the wild ass.

The desert horse is the Pleistocene animal identified by Richard Owen as an ass (*E. asinus fossilis*), but considered to be a horse by Ewart and named by him *E. gracilis*. This is a small animal, not over 12.2 hands in height, slender-limbed, with long, slender front cannon bones (Mtc. III), the length being $7\frac{1}{2}$ times the width. The head is small, the face fine and narrow, with a straight profile only slightly deflected upon the cranium. The internal cusp (protocone) of the upper molars is short. Remains of an animal of this type are found in the Pliocene of Italy (small, slender-limbed varieties of *E. stenonis*) and France, and in the Pleistocene of France and northern Africa. It agrees, so far as known, with the existing Celtic pony type (*E. caballus celticus*), a variety of

¹⁰³ EWART: *Op. cit.*

horse distinguished by small, fine head, large eyes, slender limbs, five lumbar vertebræ, now found in more or less pure form in the outlying islands and on the coast of western Europe. This animal is believed to be a northern, hardy, thick-coated relative of the pure *desert* type, better known as the Arabian, which gave rise to the modern thoroughbred. Perfect representations of this type of horse are found in the engravings and mural paintings of the Magdalenian artists in the caverns of Font de Gaume, Combarelle, and Grotte de la Mairie.

A possible contributory to the desert breed of the Pleistocene and of the modern domesticated horses is the animal of the *E. sivalensis* type of the Upper Pliocene in the Siwaliks of India. This animal is tall, with long, fairly slender limbs, long neck, well elevated tail, long face, which is strongly deflected on the cranium with a slightly convex profile and broad brow, and teeth with a narrow protocone.

Bears.—The Postglacial bears (*Ursus spelæus*) are found in greater abundance than the lions. They include a gigantic and a smaller variety. The former (*Ursus spelaus*) nearly equalled the larger recent bears in size and were more thick-set and of heavier proportions; the front paws especially were of tremendous size. During a long period the cave bears undoubtedly haunted the caverns undisturbed by Palæolithic man and developed certain peculiarities of structure in these haunts: thus the claw-bearing phalanges are feebly developed, indicating that the claws had partly lost their prehensile function; the anterior premolar teeth are practically vestigial; the cusps of the grinding teeth are blunted in a way which is indicative of an omnivorous diet. It would appear, therefore, that the large herbivorous mammals and even primitive man found no very formidable enemy in the cave bear. While the other and smaller races were contemporary, there are certain indications that the smaller race (*Ursus sub-spelaus*) was geologically older, being found at Mosbach during the Second Interglacial Stage. Both races became extinct during Postglacial times without leaving descendants.

The ancestor (*Ursus arctos priscus*) of the brown bear of Europe, by some believed to be a descendant of the etruscan bear (*Ursus etruscus*) of the First or Norfolkian Interglacial Stage, is also occasionally found in the Pleistocene cave deposits. It is not so large as the cave bear and while it has been mistakenly identified with the American grizzly (*U. horribilis*) in reality it has closer affinities to the European brown bear (*Ursus arctos*).

The badger (*Meles taxus*) also probably originated in west-central Asia, since the only other species known are confined to Asia. The two

extinct Lower Pliocene species are found in Maragha, Persia (*M. polaki*, *M. Maraghanus*).¹⁰⁴

TRANSITION TO THE EUROPEAN FOREST STAGE

This transition is believed to have begun late in Postglacial times, toward the end of the Magdalenian culture period. Evidence that the mammoth fauna lingered late both in the Dordogne region of central France and to the north is found in the abundant representation of the mammoths in the very latest paintings and engravings by the Magdalenian artists.

MIGRATION OF THE TUNDRA FAUNA

The backward or northward migration of the Tundra fauna is believed to have occurred in the following manner.¹⁰⁵ As the glacial caps retreated they left barren stretches behind them and the valleys and plateaus now free from ice became tundras where swamps alternated with patches of polar willows and stunted fir trees, while other areas were covered merely with low, scrubby birches or reindeer moss and lichens. As these climatic conditions shifted northward before the retreat of the great Scandinavian glaciers the Tundra fauna followed. It was a slow change that drove the Tundra mammals toward the dry regions of the east to make room for the forests and their faunas advancing from the south. It is clear that the north and east were the only directions of retreat for the damp climate and the spread of the woodlands.

RETREAT OF THE STEPPE FAUNA

As long ago as 1890 Nehring¹⁰⁶ held that the Steppe period of central Europe was partly in Postglacial times. This opinion was supported by Woldrich (1896),¹⁰⁷ and has been abundantly confirmed by Harlé's observations in southern France and by the recent researches of Koken and Schmidt. Steppe conditions of climate appear probable from the extensive depositions of the "Newer Loess" in Postglacial times (Koken,

¹⁰⁴ SCHARFF, R. F.: *The History of the European Fauna*, p. 44. London, 1899.

¹⁰⁵ STUDER, T.: "Die Tierreste aus den pleistocänen Ablagerungen des Schweizersbildes bei Schaffhausen." *Neue Denkschr. allg. schweiz. Ges. Gesam. Naturwiss.*, Vol. xxxv, pp. 1-38. 1896.

¹⁰⁶ NEHRING, A.: *Über Tundren und Steppen der Jetzt- und Vorzeit, mit besonderer Berücksichtigung ihrer Fauna*, pp. 81-166. Berlin, 1890.

¹⁰⁷ WOLDRICH, J. N.: "Ueber die Gliederung der anthropologischen Formationsgruppe Mitteleuropas." *Sitzber. kgl. böhm. Ges. math. naturwiss. Class.*, 1896. *Ref. Matiegka in Centralblatt Anthropol.*, pp. 142-143. 1896.

Schmidt). On the other hand, Kobelt¹⁰⁸ and Scharff¹⁰⁹ agree in thinking that the presence of Steppe mammals affords inadequate proof of the steppe character of the country in Inter- and Postglacial times. The deposits of the "Newer Loess" in Postglacial times point to a dry steppe period because according to the theory of Richthofen, which is now generally accepted, the loess owes its origin to wind-borne dust and sand acting under the influence of a dry climate either in summer or winter.

The Steppe Fauna in deposits at several points is shown to have lingered longer than the Tundra fauna. As regards the lingering of the Steppe Fauna it is indicated in the succession of the three rodents characteristic of the Tundra, Steppe and Forest conditions respectively, namely:

Forest climate and conditions, the squirrel (*Sciurus vulgaris*)

Steppe climate and conditions, the jerboa (*Alactaga jaculus*)

Tundra climate and conditions, the banded lemming (*Myodes torquatus*)

The absence of fossil plants in the deposits of the steppe period is due to the unfavorable conditions for the preservation of plant remains. Small stretches of woodland were probably confined to the banks of rivers, to favorable mountain slopes, etc. The flora was probably like that of eastern Eurasia or southwestern Siberia to-day. In their migrations such animals as the jerboa which were unable to swim presumably crossed the rivers while frozen over.

Saiga.—Of the Steppe fauna (fully described on p. 248) the saiga antelope (*Saiga tartarica*) has at the present time retreated to the steppes of eastern Europe and western Siberia. This animal is represented in the carvings and engravings of Upper Palæolithic or late Magdalenian times in the Dordogne region of France. Its fossil remains have been found in thirteen localities in southwestern France in association with a cold steppe fauna. In the same region have been found remains of the musk ox (*Ovibos*).

SURVIVAL OF FOREST AND MEADOW FAUNA

The final retreat of the cold faunas of the tundras and steppes occurred during the late stages of the Upper Palæolithic Magdalenian culture. The most advanced Magdalenian art continues to represent the woolly mammoth in the cavern of Font de Gaume (Dordogne) and elsewhere, but in the very latest Magdalenian culture stages it would appear that the mammoth and woolly rhinoceros were becoming rare. This final

¹⁰⁸ KOBELT, W.: Die Verbreitung der Tierwelt. Gemässigte Zone. Leipzig, 1902.

¹⁰⁹ SCHARFF, R. F.: The History of the European Fauna. London, 1899.

Magdalenian culture, which is correlated with the Gschnitz advance (Schmidt, *op. cit.*, p. 270), is later than the Steppe period of the "Upper Rodent" layer, which is correlated with the preceding Bühl advance.

At the same time the Crô-Magnon, or Aurignacian type of *Homo sapiens*, which we believe to be the artistic race of the Reindeer period, disappears or becomes greatly reduced in numbers and new brachycephalic and dolichocephalic races of men enter Europe.

Azilian-Tardenoisian, Final Upper Palæolithic Culture.—This is regarded as the closing culture of Upper Palæolithic times. It is believed to be associated with the newly arriving broad-headed *Furfooz-Grenelle* race. Although this point is not positively determined this race is first found at Ofnet in Bavaria. It is readily distinguished from the preceding Magdalenian culture by the degeneration of the stone industry into microlithic and other types and by the entire disappearance of art in all its forms. The Azilian culture is essentially Palæolithic although it embodies only its last degenerate stages. While the perfection of the older crafts was lost forever the Neolithic arts of polishing stone, making pottery, cultivating land and domesticating animals are as yet utterly unknown. The Azilian is the age of the stag for there is no longer any trace of the reindeer or other Tundra forms. The bone implements are now made of the horns of the stag. The Tardenoisian culture, supposed by some to be distinct from the Azilian, is characterized by flint microliths of unusual fineness, but it appears that the Azilian and Tardenoisian cultures are contemporary (Obermaier, 1912).

There were two or more human races in Europe in these pre-Neolithic times including brachycephalic and dolichocephalic types which are found commingled at Furfooz. In the meantime Palæolithic races were advancing in the north along the shores of the Baltic and preceding the Campignian culture, which is the first of the Neolithic arrivals in the Baltic region.

Forest Fauna.—The spread and multiplication of the Eurasiatic Forest Fauna thus occurred before the close of Palæolithic times. Following the retreat of the glaciers and the disappearance of steppe conditions of climate there came a gradual subsidence of the coasts of northern Europe and with it a more humid climate favorable to reforestation. Besides the common squirrel (*Sciurus vulgaris*) which is the herald of forest conditions all over the northern hemisphere, there appear in larger numbers the entire Forest Fauna which we have traced from its beginnings in early Pleistocene times and which we regard as having been resident in favorable localities throughout the entire epoch. With the Tundra and Steppe Faunas disappear also the wolverine (*Gulo luscus*) and the lion

(*Felis leo spelæa*), which are never found in western Europe after the Pleistocene although the lion lingered until a late period in eastern Europe.

The Alpine Fauna, which is mainly of central Asiatic rather than of northern relationships, retreats to the higher levels of the Alps and the Pyrenees. Thus there remained in the forests, in the plains and in the lower mountain regions of Europe the direct descendants of the Eurasiatic Forest and Meadow Fauna of the Pleistocene. It is noteworthy that no new mammals appear in Europe at this time except those introduced by man. The fauna of early Neolithic times is directly sequent upon that of late Palæolithic times. This fauna has been discovered in the Swiss lake dwellings¹¹⁰ (Fig. 9, 38-40) at Moosseedorf, Wauwyl, Robenhausen, Concise, etc. In the peat bogs of Hassleben (41), etc., in the travertines of Jena, Langensalza (42), etc.,¹¹¹ have been found the following mammals:

FOREST AND MEADOW

Bison bonasus, the European bison, still surviving in Lithuania.

Bos primigenius, collateral ancestor of the long-horned larger existing cattle of western Europe. The "*urus*," of Cæsar's text. Surviving in Germany until the sixteenth century.

Bos longifrons, the "Celtic short-horn," the probable ancestor of the small breeds of British short-horned and hornless cattle.

Cervus elaphus, the red deer or stag.

Cervus capreolus, the roe deer.

Alces machlis, the elk or moose.

Rangifer tarandus, the reindeer, surviving in central Europe until the twelfth century.

Cervus dama, the fallow deer.

Sus scrofa ferus, the wild boar.

Sus scrofa palustris, the turf pig.

Equus caballus celticus, the Celtic pony, representative of the "plateau" type.

Equus caballus typicus, the Norse, or "forest" horse.

Castor fiber, the beaver.

Sciurus vulgaris, the common squirrel.

Lepus timidus, the European hare.

Lepus variabilis, the arctic hare, in Ireland and the north.

Mus sylvaticus, the field mouse.

Arctomys marmotta, the marmot of the alpine fauna.

Ursus arctos, the brown bear.

Meles taxus, the badger.

¹¹⁰ RÜTIMEYER, L.: "Die Fauna der Pfahlbauten der Schweiz," Neue Denkschr. allg. schweiz. Gesell. gesam. Naturwiss., Vol. XIX. Zürich, 1862.

¹¹¹ POHLIG, H.: "Vorläufige Mittheilungen über das Plistocæn, insbesondere Thüringens," Sitzungsber. Niederrhein. Ges. Bonn, pp. 2-15. Mar. 3, 1884.

Mustela martes, the pine marten, also the weasel, pole cat, the ermine, etc.
Lutra vulgaris, the otter.
Gulo luscus, the wolverine.
Canis lupus, the wolf.
Canis vulpes, the fox.
Felis catus, the wild cat.

ALPINE

Capra ibex, the ibex of the mountain or alpine fauna.
Rupicapra tragus, the chamois of the mountain fauna.

There is evidence of the "plateau" or "Celtic" horse in the Neolithic deposits of Essex and of Switzerland (La Tène); it was widely distributed in Europe and Asia in prehistoric times.¹¹²

It is beyond the purpose of this volume to trace the history of domestication. The dog (*Canis familiaris*), a descendant of the wolf (*Canis lupus*), first appears in western Europe late in Upper Palæolithic times.¹¹³ The Neolithic immigrants, or men of the New Stone Age, possessed or brought with them cattle, sheep, goats, pigs, horses and dogs. Appreciating the value of domestication, they certainly captured and domesticated three indigenous European species, namely, the Celtic short-horn cattle, the forest horse (*E. caballus typicus*) and the Celtic horse (*E. caballus celticus*). The wild ox (*Bos primigenius*) was hunted but not domesticated. The domestic ox (*Bos taurus*) shows many points of resemblance to the *Urus*, but is not directly descended from it, but rather from the *Bos trochoceros* type of the Pleistocene of Italy. Rüttimeyer has made an exhaustive study of this subject,¹¹⁴ tracing the origin of the various types of domesticated cattle.

¹¹² EWART, J. C.: *Op. cit.*, 1907.

¹¹³ E. TROUËSSART considers the diminutive wolf of India, *Canis pallipes*, as the principal if not the sole source of all our races of domestic dog. This species of wolf, with the exception of the Sumatran wolf, *Canis sumatrensis*, is also more closely related than any other to the dingo of Australia. "L'Origine préhistorique du chien domestique," *Revue des Idées*, pp. 388-411. June 15, 1911.

¹¹⁴ RÜTIMEYER, L.: "Die Fauna der Pfahlbauten der Schweiz," *Neue Denkschr. allg. Schweiz. Gesell. gesam. Naturwiss.*, Vol. XIX. Zürich, 1862.

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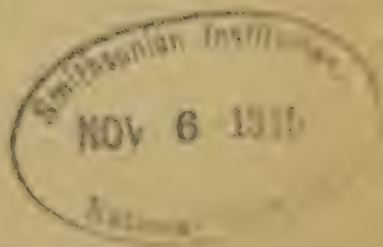
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PRESENT STATUS OF THE PROBLEM OF
THE ORIGIN OF THE TETRAPODA

WITH SPECIAL REFERENCE TO THE SKULL
AND PAIRED LIMBS

BY

WILLIAM K. GREGORY



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PRESENT STATUS OF THE PROBLEM OF THE ORIGIN OF THE TETRAPODA, WITH SPECIAL REFERENCE TO THE SKULL AND PAIRED LIMBS¹

BY WILLIAM K. GREGORY

*(Presented before the Academy, 13 February, 1911, 13 November, 1911,
11 December, 1911, and 10 February, 1913)*

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COMPARATIVE STUDY OF THE SKULLS OF PRIMITIVE FISHES AND STEGOCEPHALI

INTRODUCTION

The researches of Credner, Thévenin, Fritsch, Moodie and many others on the amphibians of the Coal Measures, which are the oldest known Tetrapoda, have served on the whole to bring into clearer focus the wide structural hiatus that is still left between the known Amphibia and the known fishes. For the former without exception have the paired limbs, when present, in the form of cheiropterygia; while in the latter the

¹ Manuscript received by the Editor, 6 March, 1915.

paired limbs are still incontestibly ichthyopterygia; and there are almost equally great differences in the skull.

Baur's view that the Amphibia and higher classes have been derived from Palæozoic Crossopterygii has of late years been supported especially by Watson (1912) and Broom (1913). Jaekel (1896, 1909), who delights in such phylogenetic paradoxes, holds that the earliest Tetrapoda, instead of having been derived from the fishes, have given rise to them through progressive secondary adaptation to aquatic life.

Although the true linking forms between fishes and amphibia still remain unknown and must be sought in formations of Lower Devonian or even Upper Silurian age (Moodie), comparative anatomy alone offers sufficient evidence to prove that the recent fishes and Tetrapoda, in spite of their admittedly wide differences and remote separation, yet trace their origin to a common source. One need cite only the fundamental unity of plan that runs throughout the vertebrate series and the weighty characters that unite all the Craniata into a natural group. One recalls, for example, that creatures so diverse in form and mode of life as fishes, amphibians, reptiles, birds and mammals all have an identical arrangement of the six eye-muscles in relation to the eyes and to three of the cranial nerves; that the complex head is a synthesis of sensory capsules, brain-trough, occipito-vertebral segments, primary jaws, branchial arches and dermal elements; that the whole locomotive and muscular apparatus of trunk, limbs and head is evolved out of metamerically arranged myomeres of identical embryonic history. Thus, although the differences between known Amphibia and known fishes are very marked, they are morphologically of far less weight than the resemblances.

The main conclusion of the present paper is that among the various groups of fishes which are known from the Devonian and Upper Silurian, only one, the rhipidistian Crossopterygii, belongs near the ancestral line or lines of the Tetrapoda.

OSTRACODERMI, ANTIARCHI AND ARTHRODIRA

As the Silurian and Devonian Ostracodermi include the oldest known types of chordate animals it is pertinent to inquire what their relations may be to the remote ancestors of the Tetrapoda. All the known ostracoderms appear to be aberrantly specialized in certain directions, but long consideration of their many peculiar characters has convinced me that they stand far below the true fishes and that the group as a whole may represent an important stage in the genealogy of the vertebrates.

Of the many beautifully preserved specimens of *Birkenia*, *Lanarkia*, *Drepanaspis*, *Pteraspis*, *Tremataspis*, *Cephalaspis* and allied genera, none

show the least indication of an internal skeleton, nor is there ever any trace of branchial arches and internal jaws. The pouch-like markings on the inner side of the carapace in *Pteraspis*, the large sack-like markings in *Thelodus pagei*, the small round gill openings of several genera indicate a branchial apparatus somewhat similar to that of the larval *Petromyzon*. The median opening in front of the paired eyes in *Cephalaspis* and its allies suggests also the median nostril of *Petromyzon*. Due caution is necessary in accepting any of these resemblances as indicative of real affinity with cyclostomes, yet they apparently give evidence of the mode of functioning of the mouth and pharynx.

In brief, the ostracoderms, instead of being free swimming predatory types, with powerful locomotive organs, strong internal jaws and true teeth, as in the later fishes and ancestral Tetrapoda, were, with the exception of the Birkeniidae, sluggish and bottom-living forms accustomed to feed on small organisms, which they obtained in the mud, or by drawing water into their capacious pharynx.

In these animals the process of cephalogenesis, or synthesis of elements into a complex head, was probably in a low stage of development, most of the "cephalic buckler" in forms like *Drepanaspis* and *Cephalaspis* representing an expanded pharyngeal region rather than a large brain, which may have been as small as it is in recent cyclostomes.

The ostracoderms represent a stage in chordate phylogeny immediately preceding the acquisition of an endoskeleton impregnated with mineral salts; their first visceral arches, if present, had not yet been transformed into primary or cartilaginous jaws; the process of cephalogenesis was in them in a low stage, and the elements of their shelly exoskeleton were potentially homologous with the cosmine, vasodentine and isopedine of primitive ganoids. To that extent they stand in a pre-gnathostome stage of evolution and probably represent the remote forerunners of the ganoids and Tetrapoda, while possibly having remote relationships also in another direction with the ancestral elasmobranchs.

The Antiarchi have advanced beyond the typical ostracoderms in having the head sharply differentiated from the thorax and the mouth armed with functional jaws, which are fashioned from the dermoskeleton. But not even the excellently preserved specimens of *Bothriolepis* described by Patten (1912) show any traces of cartilaginous jaws, branchial arches or cartilaginous axial skeleton.

The systematic position and relationships of the Arthrodira constitute so controversial a subject that it would be the part of discretion to avoid it if possible. Unfortunately this question as well as certain still larger ones cannot be altogether kept out of the discussion as to the origin of

the Amphibia. With regard to the Arthrodira I can only say that I have long pondered over the conflicting views and arguments of Smith Woodward, Eastman, Dean, Hussakof, Tate Regan, Jaekel and Patten; that I have endeavored to consider the question without bias of any kind and have returned again and again to readjust the conflicting claims of diverse evidence for the relationship of the Arthrodira: either with the Dipnoi (Eastman, Smith Woodward), or with the Antiarchi (McCoy, Dean, Hussakof), or with the Devonian Crossopterygii (Tate Regan) or finally with the stem of the Dipnoi and Amphibia on the one side and the Antiarchi, Ostracodermi and even the Arthropoda on the other (Jaekel, Patten). Out of this maze of conflicting resemblances I gain the impression that the resemblances which tend to brigade the Arthrodira with the Antiarchi are quite specific and of evidential value,² while the resemblances in the jaws and head-shield to those of Dipnoi and still more to those of Crossopterygii, are, with certain exceptions, of a vague and inconclusive character, suggestive of convergent evolution between widely removed groups. And in this connection I would call attention to the arthrodiran appearance of the skull-top of the modern armored catfish *Clarias magur* (figured by Goodrich, 1909, p. 381), as illustrating the deceptive effects of convergent resemblances; a similar example is the *Cephalaspis*-like appearance of *Loricaria*.

Until it shall be learned whether *Macropetalichthys* is really related to the Arthrodira and what its affinities are with other groups, it is hardly likely that the Arthrodira problem can be definitely settled. In the meantime I must hold provisionally: first, that the arthrodiran jaws, skull and thorax represent progressive, carnivorous adaptations from a generalized antiarchian stem; secondly, that the resemblances in the skull-roof to those of Dipnoi and Crossopterygii have been independently assumed; thirdly, that the Arthrodira are not true gnathostomes and consequently not anywhere near the line leading toward the Tetrapoda, but that they are, on the contrary, the last and highest of a pre-gnathostome adaptive radiation. In brief this pre-gnathostome radiation was characterized by an accelerated evolution of the exoskeleton of the head and thorax and by a retarded evolution not only of the endoskeleton but of the whole locomotive apparatus.

ELASMOBRANCHII

In the Acanthodii, which are the earliest elasmobranchs, the gnathostome series is first made known by its relatively advanced adaptations to predatory, free swimming habits: first, the whole pharyngeal region

² Cf. the list of common characters given by Hussakof, 1906, pp. 123-136.

is supported by a stout cartilaginous framework and the contractility of the anterior pair of arches has led to their functioning in the seizing and ingestion of the prey: secondly, the primary locomotive organs, namely, the myomeres, have much increased in number and size, the head becoming relatively small; thirdly, the paired sensory capsules (olfactory, optic, auditory) and the primitive brain-trough are synthetized into a chondrocranium, which very early affords support for the oral arches, while the more active life necessitates the strengthening of the primitive endoskeleton, an end which is attained in this group by the deposition of calcareous salts in the hyaline cartilage; fourthly, many accessory structures appear: such as median and paired fins and fin supports, fin-spines, true teeth and minute rhombic scales.

All these external improvements in the locomotive and food-getting structures were no doubt matched by corresponding increase in the size of the brain and probably by marked changes in the proportions and placement of its principal parts.

Such a transformation from pre-gnathostome to primitive gnathostome conditions was a critical step in the history of the vertebrates and makes the differences between Tetrapoda and true fish seem relatively unimportant.

The elasmobranchs are excluded from direct ancestry to the Tetrapoda by the fact that they too early overspecialized in some respects while remaining on a low stage in others: first, the exoskeleton was formed too largely from the outer layers of the many-layered skin, the deeper, stratified connective tissue remaining unossified: hence except in the *Acathodii* we see an armature of thorny denticles or placoid tubercles rather than of osseous plates and scales. And secondly, the endoskeleton, instead of becoming osseous, became thoroughly calcified.

The earliest elasmobranchs have the preorbital portion of the cranium short, the small eyes being almost terminal and not widely separated from each other, as in most of the ostracoderms, antiarchs, arthrodires, earliest ganoids and tetrapods. It is only in specialized types in all these groups that the olfactory capsule or rostrum grows forward and the eyes are displaced backward and become of large size.

So far as known the elasmobranchs lack the median opening between the orbits which is doubtfully homologized with the pineal opening in ostracoderms, antiarchs, arthrodires and primitive ganoids.

ACTINOPTERYGII

The Dipnoi, Crossopterygii and Actinopterygii (collectively known as Osteichthyes) share with the elasmobranchs on the one hand and with

the tetrapods on the other all the characters which separate the Gnathostomata from the Agnatha. But they have advanced beyond the elasmobranchs toward the tetrapod type in many particulars, especially: (1) in the appearance of true bone cells both in the exo- and endoskeletons; (2) in the formation of scales, dermal rays and dermal plates, having in the most primitive forms an outer cosmine layer, a middle zone of vasodentine and basal layers of isopedine; (3) the formerly continuous dermal covering of the head and trunk is now fragmented into the dermal plates of the skull, of the branchial region (operculars, gulars, etc.) and of the pectoral region; (4) the spiracular cleft is usually closed.

Most of the known Osteichthyes are excluded from the ancestry of the Tetrapoda by various specializations, either of the exoskeleton or of the median and paired fins as noted below.

In the Actinopterygii, a sufficiently full morphological series enables us to follow the changes in the group, beginning with the very generalized Devonian *Cheirolepis* and culminating in the most specialized types of modern teleosts. In the most primitive of the series (Palæoniscidæ) the elements of the skull-roof may be in general homologized with those of the most primitive Crossopterygii, although the details are quite different; there is, however, no special resemblance to the skull of the earliest Stegocephali, except in so far as the elements of the skull-roof include paired frontals, parietals, pterotics and other paired elements. The brain also is diversely specialized in the surviving forms.

DIPNOI

A closer structural approach to the tetrapod type is attained in this group. In the brain the Dipnoi have retained the well-developed olfactory lobes and cerebra, which are requisite for the ancestral tetrapod. They also have a functional lung and, as Kellicott (1905) has shown, the venous system presents close ontogenetic resemblances to the urodele type. The larvæ and embryos of the Dipnoi, as well as of the Crossopterygii, reveal further well-known striking resemblances to the urodeles, and, as noted below, there are many features of the locomotive organs and mode of locomotion in Dipnoi that foreshadow the conditions in Tetrapoda. While much of this might be ascribed to convergence, it all implies a similarity in the "potential of evolution," that is, of structural possibilities, in the forerunners of these groups.

The known Dipnoi are all excluded from direct ancestry to the Amphibia by the specialized character of the dentition, including the formation of complex radially arranged tritoral plates on the roof of

the mouth and on the inner side of the mandible and the loss of marginal teeth on the premaxillæ, maxillæ and dentaries.

The earliest Dipnoi have "paralleled" the Tetrapoda and other progressive types in that the preorbital rostrum is expanded and the orbits are relatively far posterior though still of small size; the pattern of the skull-roof, with its paired "frontals," "parietals" and other elements, is also probably analogous, rather than homologous, with that of Tetrapoda.

Our conception of the relationship of the Dipnoi to the Tetrapoda is

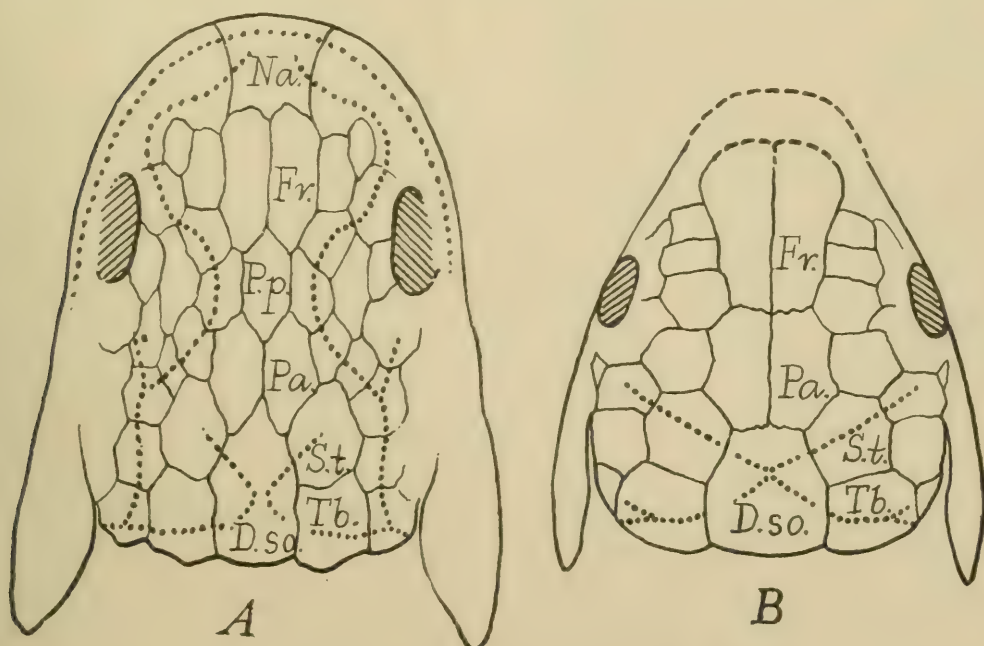


FIG. 1.—Pattern of skull-top of Devonian dipnoans

A, *Dipterus*, after Goodrich, slightly modified; B, *Scaumenacia curta*, after Hussakof.

In specimens of *Dipterus* the numerous sensory pits are scattered over broad tracts, the general directions of which are indicated by the dotted lines, except in the occipital region where the dotted lines represent shallow grooves. The principal sensory tracts are in general similar to those of Stegocephali.

The "parietals," "frontals," etc., are probably analogous rather than homogenous with those of Tetrapoda.

Dso, dermosupraoccipital; *St*, supratemporal (pterotic); *Tb*, tabulare (epiotic); *Pp*, preparietal; *Fr*, frontals; *Na*, naso-ethmoid region.

to some extent dependent upon the validity of Dollo's view (1895) that *Dipterus* is the most primitive known Dipnoan, structurally ancestral to all the later types. The skull top of the modern *Ceratodus* is so widely different from that of *Dipterus* that Dr. Eastman (1907, p. 95) has concluded that the two forms have no near relationships with each other and that the living genus represents some other and independent line that has come down from a pre-dipterine stock. But after comparing the skull patterns of *Ceratodus*, *Ctenodus*, *Phaneropleuron* and *Scaumenacia*

I incline to the opinion that Dollo's view is the correct one. The skull pattern of *Scaumenacia*, as figured by Hussakof (1912, p. 136), is sufficiently close to that of *Dipterus* (Pander, 1858, Tab. 3) to enable one to homologize the principal bony elements in these two genera (Fig. 1). The *Scaumenacia* skull, I think, points the way to that of *Phaneropleuron* (Goodrich, 1909, p. 239) and this in turn brings us within reach of the *Ceratodus* skull-pattern. In short it appears probable that the *Ceratodus* skull-pattern has been derived from a *Dipterus*-like type through the following changes: (*a*) the small frontals and parietals have become enlarged, so as to cover the median, pre-parietal element; (*b*) the opposite frontals have united to form the wrongly called "ethmoid" of *Ceratodus*; (*c*) the opposite parietals have united with each other and with the median supraoccipital or nuchal plate to form the large median "occipital"; (*d*) the longitudinal series of small elements running from above the orbits to the back of the skull have coalesced and broadened, to form the large pair on either side of the median plate; (*e*) the small plates behind the orbit and above the operculum have coalesced and broadened into the large plate marked pterotic in Goodrich's Fig. 206 (1909, p. 237); (*f*) the remaining small elements immediately behind the orbit are part of the circumorbital series; (*g*) the exposure of the chondrocranium above the occiput and above the front part of the skull I regard as quite secondary and as a relatively modern specialization; the massive character of the chondrocranium may be due to the fact that the stout tritoral plates on the roof of the mouth and the heavy mandible require a massive firm skull for their support: it may also be related with the fact that the scales and dermbones of the skull are losing their dense osseous character and becoming horny. The exposure of the chondrocranium is carried to an extreme in *Lepidosiren*, and it cannot be claimed that this degenerate, eel-like form is more primitive than the numerous Palæozoic Dipnoi, Crossopterygii and Actinopterygii that have a complete skull-roof.

In view of the foregoing discussion it is hardly necessary to state that I am unable to accept Dr. Eastman's comparison (1907, p. 132) of the *Ceratodus* skull with that of *Dinichthys* at its face value, and, with Dr. Dean (1907), I must ascribe these resemblances to convergence, referring again to the arthrodiran appearance of the skull-top of one of the modern catfishes (*vide supra*, p. 320).

Returning to *Dipterus* I would also be inclined to disagree with Goodrich's statement (1909, p. 256) that "the arrangement of the cranial covering bones points rather to the dipterids being a highly specialized offshoot from the base of the dipnoan stem." As already stated, the

Dipterus skull-top certainly includes the same elements as those of *Scaumenacia*, the chief difference being that these elements are smaller and that there are a number of other small elements in the supraorbital-occipital series, which may later have united with adjacent elements. The *Dipterus* skull-top also makes a distant approach to the primitive rhipidistian type seen in *Osteolepis*, in so far as it retains lines of sensory pits running longitudinally above the orbits and extending back to the transverse nuchal commissure: both skulls also have a circumorbital series, a supraorbital-occipital series, a short rostrum, paired frontals, parietals and other paired elements, the chief difference being that in *Dipterus* there is a prominent median preparietal and that the nuchal plates are more closely united with the occiput.

The conclusion that *Dipterus* is the most primitive of all the Dipnoi is further supported by the remarkable agreement in histological structure of the dermoskeleton of *Dipterus* and that of the crossopterygian *Osteolepis* as shown in Pander's superb sections (1858, Tab. 5, Figs. 1, 17; 1860, Tab. 5, Figs. 1-8, 22). In both cases the dermocranium consists of a thin outer layer of ganoine, which covers the cosmine layer, underneath this is a vascular layer and on the bottom a stratified horizontal layer. This histological pattern is also repeated in the scales of both *Dipterus* and *Osteolepis*, and to my mind is of great weight in indicating the common origin of the Dipnoi and Crossopterygii. Add to that the facts: that in both groups the earliest members have the paired fins of the mesorhachic or biserial type; that both have two dorsal fins: that both have a heterocercal tail provided with similar dermal rays, and we have a case for the common origin of the Crossopterygii and Dipnoi, which is further strengthened by the well known resemblances between the modern *Polypterus* and the dipnoans in the early stages of development. Nor should the differences in brain structure of these modern forms outweigh the above mentioned resemblance, for there is no evidence that the brains of the Devonian Crossopterygii and Dipnoi were any more divergent from each other than were the other parts of the body.

CROSSOPTERYGII

The known Dipnoi being excluded from direct ancestry to the Tetrapoda by reason of certain specializations of the skull and dentition, what can be said of the claims of the Crossopterygii?

Polypterus, and doubtless also its near ally *Calamoichthys*, which are the only surviving crossopterygians, have become highly ichthyized in brain characters and thus are far removed from both the dipnoan and the amphibian types; but as stated above it may well be that the Devonian

Crossopterygii had a more primitive brain structure. In *Polypterus* the scales and dermal plates have become like those of the primitive Actinopterygii (Goodrich 1909, p. 292), the cosmine layer being covered externally by stratified ganoine layers; but for several reasons I regard this condition as secondary. Nor can I accept Goodrich's view (1909, p. 300) that *Polypterus* should be removed altogether from the Crossopterygii. In any event it is further removed from relationship with the Tetrapoda than were its Devonian predecessors.

The only crossopterygians that can claim even remote relationships with the Amphibia are the Devonian Rhipidistia, especially the Osteolepidæ and the nearly allied Rhizodontidæ. Dr. A. S. Woodward's comparison (1898, pp. 24, 25) of the skull-roof of *Rhizodopsis*, representing the Rhizodontidæ, with that of *Pelosaurus*, representing the Stegocephalia, serves, however, to emphasize the remoteness of this relationship and to raise the question whether the supposedly homologous elements, as the frontals, parietals etc., in the two groups, may not after all be analogous rather than truly homogenous. Dr. Moodie's comparison (1908) of the sensory canals of the skull-roof of stegocephalians with those of *Amia* and *Polypterus* offered some reinforcing testimony, which would have been strengthened if Pander's superb figures showing the sensory pits and skull elements of *Osteolepis*, *Diplopterus*, *Dipterus* and other genera had been taken into consideration. Watson's comparisons (1912) of the skull-base of *Rhizodus* with that of certain Carboniferous stegocephalians (*Pteroplax* etc.) having a single median occipital condyle and a continuous or non-fenestrated palate, further strengthened the case.

A wider basis of comparison appearing desirable, I have made during the last few years repeated comparison of the skull patterns of various Palæozoic and recent fishes with each other and with those of stegocephalians of all known orders. Original material of *Osteolepis*, *Megalichthys*, *Dipterus* and of many other fossil and recent Osteichthyes has been studied, and for the skull patterns of many of the Palæozoic fishes I have also had recourse to the excellent figures of Pander, Huxley, Traquair, Smith Woodward, Goodrich, Wellburn (*Megalichthys*), Jaekel (*Diplopterus*) and others. Similarly among the Stegocephali the American Museum collections have furnished for study typical examples of the principal groups; and in making comparisons with the fishes I have also had before me the figures of Credner, Fritsch, Moodie, Fraas, Embleton and Atthey (*Loxomma*), Watson, Broom, Williston and others.

Before considering in detail the skull-roof in primitive fishes and Tetrapoda, it may be appropriate to ask whether any general adaptational reasons can be assigned provisionally for the several characteristic ar-

rangements of the sutures which produce the distinctive skull patterns of these early types. It was recognized by Ryder (1892) that the shape and arrangement of the scales of fishes was originally a result of the movements of the myomeres, but so far as I know it has not hitherto been taught that the shape and arrangements of the dermocranial elements, which in primitive fishes are histologically homologous with scales, were likewise the result in part of muscular strains and stresses. It may be stated as a general hypothesis that *in the dermocranium of primitive fishes the position and arrangement of the sutures and the consequent pattern of the osseous "elements" are the evolutionary resultants of the various symmetrically balanced stresses induced by the action of the underlying muscles of the eyes, jaws, branchial arches and pectoral limbs. in composition with the position and size of the olfactory, optic and auditory capsules. It is at least a fact that sutures and other articulations define loci of relative mobility, centers of ossification define loci of relative stability. Differential growth of one region of the skull, as in the rapid elongation of the snout, also results in more or less rearrangement of the sutures and osseous elements.*

I would also advance the hypothesis that the whole dermoskeleton of the head in the unknown pre-Devonian forerunners of the Dipnoi, Crossopterygii and Actinopterygii was a continuous membranous covering, consisting (see Goodrich, 1909, pp. 215-217) of minute cosmine tubercles underlain by imperfectly differentiated vasodentine and isopedine and entirely homologous with the membranous covering of the trunk and fin-folds. Wherever movements of this membranous covering were pronounced, as in the opercular region, around the orbits and near the spiracular clefts, there were deep creases, but where movements were less pronounced the creases were proportionally shallow. When the critical stage of ossification began, in the forerunners of the Dipnoi, Crossopterygii, Actinopterygii, the roof of the dermocranium commenced independently in the several lines a process of fragmentation; so that the rostrofrontal segment was split up into premaxillæ, nasals, ethmoids, frontals; and the orbito-parietal segment was divided into its component "elements."

The excessive subdivision of the maxillary and preoperculum of *Lepidosteus*, of the parafrontals of cœlacanths, of the spiracular plates of *Polypterus* furnish extreme examples of fragmentation. In the skull-roof of *Osteolepis*, on the other hand, we may have an example of a form in which ossification of the dermocranium had already taken place, but fragmentation of the "cranial buckler" was still incomplete. In some specimens of *Osteolepis* the median suture between the frontals extends

forward nearly to the tip of the rostrum; in others it is much shorter; none have the separate nasals which appear in higher types; on the other hand, the transverse occipital row of small plates (see below, p. 329) seen in *Osteolepis* and *Gyroptychius*, are barely indicated in *Tristichopterus* and had not split off in *Rhizodopsis* or *Megalichthys*.

As the conical teeth of Crossopterygii were on the outer margins of the jaws and the movements of the jaws were chiefly vertical, the suggestion may perhaps be hazarded that the transverse stresses conditioned the evolution of the longitudinal median sutures, while the anteroposterior stresses resulted in transverse sutures, those separating the rostro-frontal and postorbito-parietal segments being in *Osteolepis* particularly deep. At any rate the resulting skull pattern includes many more or less rectangular plates, as also in the Actinopterygii. In the primitive Dipnoi, on the other hand, the teeth were clustered in fan-like ridges on the roof of the mouth and the movements of the jaw were more oblique; this possibly may have partly conditioned the oblique character of the skull-roof sutures and the polygonal form of the elements. In the Stegocephali both rectangular (*e. g.*, *Branchiosaurus*) and oblique (*e. g.*, *Stegops divaricata* Moodie) types occur.

After the primary sutures had been established and the continuous dermocranium fragmented into small plates, there usually followed an enlargement of certain plates, and sometimes a coalescence of adjacent plates, as in the Dipnoi and other groups of fishes: such enlargement and coalescence following *ex hypothesi* not only upon the shifting of lines of greatest mobility or the diminution of mobility between elements, but also from the circumstance that as a general rule in evolutionary series, after individual structures have been differentiated out of a former continuum they appear to acquire a certain evolutionary initiative, so that they may enlarge or decrease or shift their position, or crowd apart their fellows in a manner strongly hereditary, but often without any assignable, immediately adaptive purpose.

The position and apparent homologies of the elements of the skull-roof in the Rhipidistia, in comparison with other primitive fishes and with the Stegocephali, are as follows:

The orbits in primitive Crossopterygii are small and sometimes far forward (*Osteolepis*, Fig. 2), quite near the front of the nasal rostrum, which is extremely short and obtuse; the same is also true of the most primitive Actinopterygii (Palæoniscidæ). The roof of the nasal rostrum (ethmoid) is undivided and there are no paired nasal bones. The short frontals, lying between the orbits, almost form part of the rostrum. Between them in some genera (*Osteolepis*, *Glyptopomus*, *Diplopterus*)

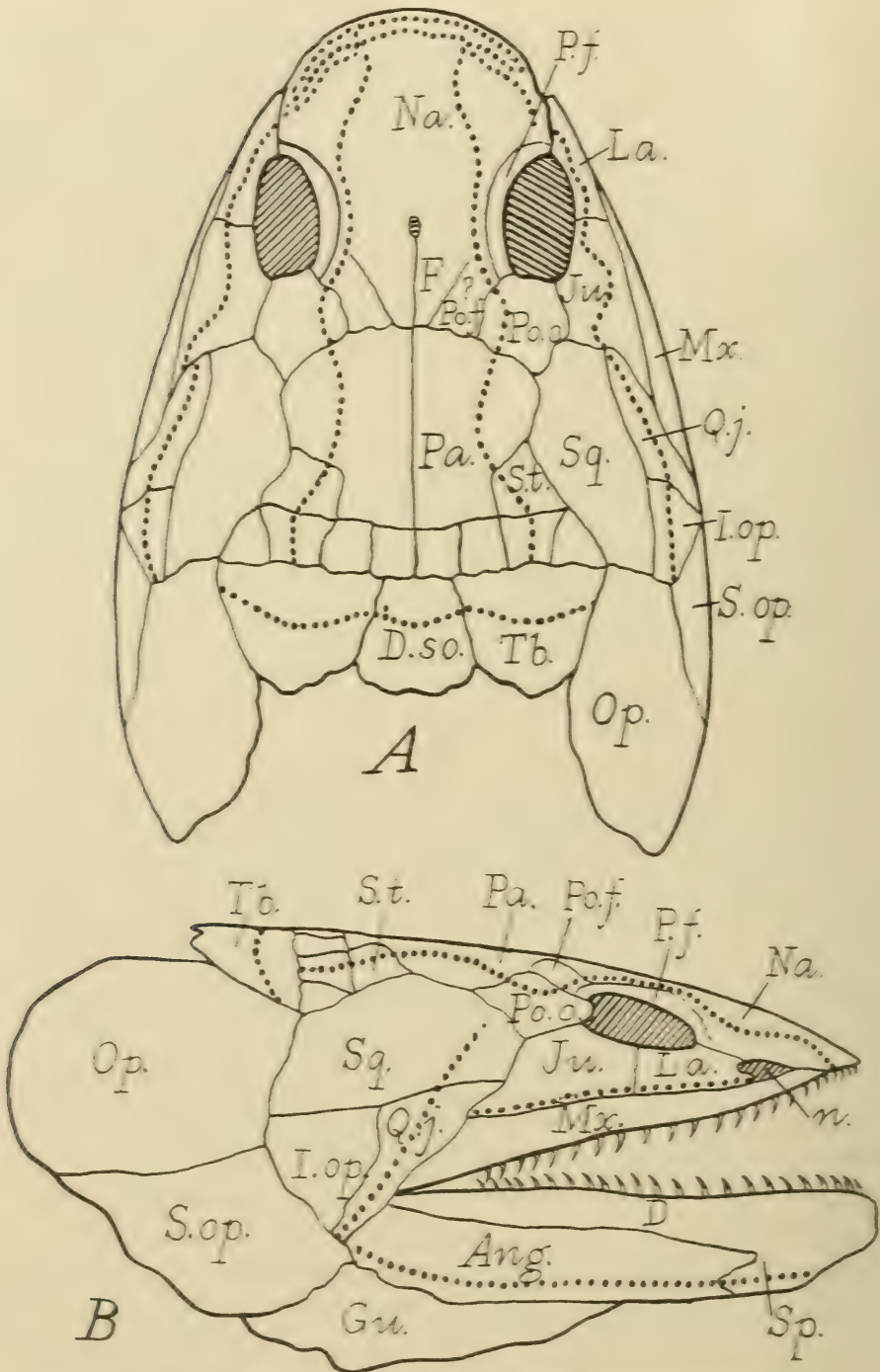
lies a foramen opening into a median tube (Pander, 1860, Tab. 5, Figs. 1-5) which has been identified by authors (*e. g.* Newberry, Dean, Jaekel) as the pineal foramen. In *Dipterus* also the frontals are short, but in the Palæoniscidæ they are longer. The postfrontals in Osteolepidæ and Rhizodontidæ are elongate narrow elements extending from the postero-superior margin of the orbits to the pterotics ("squamosals").

The parietals in the Rhipidistia are longer than the frontals, from which they are separated by sharp transverse sutures. In *Dipterus*, on the other hand, the parietals were short, in Palæoniscidæ they were short and wide.

Behind the parietals in *Osteolepis microlepidotus* (Pander, 1860, Tab. I) was a transverse series of small quadrangular elements, closely appressed to the parietals and "pterotics," which at first sight suggest the transverse occipital series of Stegocephali. The innermost or median pair of this series suggests the paired dermosupraoccipitals or postparietals of Stegocephali; next to these comes a second or middle pair; the third pair at first suggest the tabularia, and the outermost pair in the species under consideration suggest the "epiotic cornua" of such Stegocephali as *Archegosaurus*.

Nevertheless, in spite of these attractive resemblances with the transverse postparietal series in Stegocephali, I am finally constrained to treat them as analogies only. First, this transverse postparietal series is best developed in *Osteolepis microlepidotus*, is imperfectly developed in *O. macrolepidotus*, *Gyroptychius*, *Tristichopterus*, and is entirely absent in *Rhizodopsis*, *Megalichthys*, *Glyptopomus* and *Holoptychius*. But structures that are developed only in a few forms, rather than in whole groups, offer very unsafe guides for homologization with similar elements in other widely separated groups, a principle too often neglected by comparative anatomists. Secondly, this transverse occipital series in *Osteolepis* does not bear a transverse line of sensory pits, as it should do if it were homologous with the transverse postparietal series of Stegocephali (*cf.* Moodie, 1908). Thirdly, there is another row of transverse plates constituting the nuchal or "supratemporal series," lying behind the occipital suture, which bear a transverse sensory line and are homologized by all authorities with the postparietal row in Stegocephali. This nuchal series may terminate dorsally either in a single median plate, as in Dipnoi, all Rhipidistia, many Actinopterygii (? supraoccipital), or in double or paired median plates, as in *Polypterus*, *Amia*, *Lepidosteus* and all Stegocephali.

Concerning the nuchal series in *Tristichopterus alatus*, one of the Rhizodontidæ, Traquair (1875, p. 386) wrote as follows:

FIG. 2.—Skull pattern of *Osteolepis microlepidotus*

A primitive Devonian rhipidistian.

After Pander, but with revised identification of elements.

A, Top view. B, Side view.

Supposed homologies with the skull elements of Tetrapoda are indicated by the abbreviations.

Dorsal series: Na, naso-ethmoid region; F, frontal region with median foramen; Po.f., postfrontals; Pa, parietals; behind the parietals are the parieto-occipital series, perhaps not differentiated in Tetrapoda, as they lack the occipital commissure of sensory pits (see text).

Circumorbital series: P.f., prefrontal; La, lacrymal; Ju, jugal (suborbital); Po.o., post-orbital.

Temporal series: St, supratemporal (pteroptic); Sq, squamosal (preoperculum, cheek plate "X").

Gnathal series: Mx, maxilla (the premaxilla is not separated from the naso-ethmoid mass); Q.j, quadratojugal (anterior interoperculum, cheek plate "X"); D, dentary; Sp, splenial (anterior infradentary); Ang, angular (middle infradentary).

Opercular series (lost in Tetrapoda): Op, operculum; S.op, suboperculum; Gu, gular; I.op, interoperculum (? may have fused with quadratojugal in Tetrapoda).

Nuchal-occipital series: D.so, dermosupraoccipital (postparietal, median supratemporal); Tb, tabulare (epiotic, lateral supratemporal).

"Along the posterior margin of the cranial shield are three plates (*s. t.*, figs. 1 and 2), one mesial, somewhat polygonal in form, and two lateral, each apparently of a triangular shape. These are obviously the representatives of the three plates, which occur in a similar position in *Osteolepis*, *Glyptolemus*, *Megalichthys*, &c., and of which different interpretations have been given by different authors. In Professor Huxley's description of *Glyptolemus*,³ the mesial one is marked 'supra-occipital,' the two lateral 'epiotic.' Mr. Parker⁴ has, however, pointed out that they are dermal bones, and not to be considered homologous with those other deeper ossifications of the cranial cartilage. By Pander⁵ they are in *Osteolepis* simply designated 'Hautknochen' and considered to be equivalent to the five little plates, which in the recent *Polypterus* occur immediately behind the transverse row of supra-temporals, and between the pair of upper supra-claviculars (supra-scapulars), being in reality the first scales of the back. On the other hand, he considered the transverse chain of small plates (supra-temporal) which lie immediately behind the parietals of *Polypterus*, to be represented in *Osteolepis microlepidotus* by the narrow portion of the cranial shield, which in that species is marked off near the hinder margin by a more or less interrupted superficial transverse groove. I am myself very much inclined to the belief that the three dermal bones in question are in reality equivalent to the transverse supra-temporal chain in *Polypterus* and *Lepidosteus*, and which have their representatives as well in the amphibian Labyrinthodonta as in most Teleostean fishes; the transverse grooving across the posterior part of the cranial shield in many Saurodipterines being probably only of the nature of superficial markings."

In brief, the skull-roof of Rhipidistia may be regarded as consisting of the following regions or segments: first a rostrifrontal segment, comprising the parts which later became separated into the premaxillæ, ethmoid, nasals, frontals and postfrontals. In *Osteolepis* this is separated from the next segment by a sharply defined transverse suture. The second or parietal segment of the skull-roof includes only the elongate parietals and the wrongly named "squamosals" (pterotics). The third or occipital segment which is rarely distinct from the preceding (*Osteolepis*, etc.) consists of a transverse row of small elements, which, in spite of their resemblance to the dermoccipitals and tabularia of Stegocephali, are probably not homologous with them. The fourth or nuchal segment, which originally pertained to the pectoral girdle rather than to the skull, is sharply separated from the true occipital segment; it usually consists of a single median and a pair of lateral elements; all three of these are usually named "supratemporal," but they are probably homologous with the paired dermosupraoccipitals and tabularia of Stegocephali.

Returning to the region above and behind the orbits we find not only

³ Dec. Geol. Survey, x. p. 2.

⁴ Shoulder Girdle and Sternum, p. 19.

⁵ Ueber die Saurodipterinen, &c., des Devonischen Systems, p. 11-12. St. Petersburg, 1860.

In primitive Rhipidistia but also in *Dipterus* (Fig. 1. A) a longitudinal chain of small elements, bearing the supraorbital sensory line and extending back to the occiput. This series corresponds in position with the postfrontals, intertemporals and suprasquamosals (pteroics or true supratemporals) of Stegocephali.

The circumorbital series of Rhipidistia and primitive Dipnoi while variable in number and form likewise correspond in position, and appear to be collectively homologous with, the prefrontal, lacrymal, jugal, postorbital and postfrontal of Stegocephali.

The spiracular cleft, which in *Holoptychius*, *Osteolepis microlepidotus* and *Polypterus* as well as in *Dapedius* is located behind and above the orbit, appears to be lost in many Crossopterygii and in all Dipnoi, as well as in the Stegocephali.

The elements of the opercular series of *Osteolepis* and other Rhipidistia appear to be only partly homologizable with those of *Dipterus* (Goodrich, 1909, p. 240); in the Stegocephali this series appears to have been lost in part and in part preserved. In *Osteolepis* the preoperculum plus cheek plate (X) was external to the quadrate; it was also behind the postorbital and jugal, and below the pterotic or true supratemporal; in all these respects it corresponds perfectly with the lower temporal bone of Tetrapoda, which is by many authors identified with the mammalian squamosal. In *Osteolepis* and *Diplopterus* the preoperculum also bears a sensory tract, as does also the squamosal of certain Stegocephali (*e. g.*, *Ceraterpeton*, *Tutidanus*, Moodie, 1908). In other Rhipidistia (*e. g.*, *Tristichopterus*, *Diplopterus*, *Megalichthys*) the preoperculum has an essentially identical position, but includes two elements, a posterior one corresponding to the back part of the preoperculum of *Polypterus* and to the whole of the preoperculum of *Amia* and an anterior one (X) corresponding to the posterior row of postorbitals in primitive Holostei, as suggested by Traquair.

Below the preoperculum (squamosal) in *Osteolepis microlepidotus*, *Diplopterus*, *Megalichthys*, etc., are one or two elements (X'), together corresponding in position to the interoperculum of higher fishes, which have the topographic relations of the quadratojugal of Stegocephali and like that element also bear a sensory tract.

The retention and full development of the operculum, suboperculum, median paired and lateral gulars sharply separate the Rhipidistia from the Stegocephali. The fate of these elements is discussed below (p. 337).

The under side of the skull should, on general principles, yield important evidence bearing on the problem of the relationships of the Tetrapoda and the Rhipidistia. Unfortunately this region was not described

by Pander or Traquair and seems to be known only in *Megalichthys*. In this genus, Watson (1912, pp. 9-10) has noted the following remarkable resemblances to the very primitive Stegocephalians *Pteroplax* and *Loxomma*:

"The Basisphenoid of *Megalichthys* has sometimes carotid foramina just as in *Loxomma*. It has small but distinct basi-pterygoid processes which are, however, not provided with articulating surfaces but with sutural ones. The long parasphenoid extends forward to the premaxillæ as it may do in *Pteroplax*. Its lateral borders are in contact with the Pterygoids, to which they afford support, and the bone is connected with the roof of the skull by a fused ethmoid.

"The Pre-vomer is identical with that of '*Loxomma*' in the majority of its attachments, carries one large tusk and a pit for the replacing tooth. It meets its fellow of the opposite side, and forms the front of the posterior naris; it is doubtful, however, if it meets the palatopterygoid.

"The Palatopterygoid of *Megalichthys* is exceedingly like the palatine and pterygoid of *Pteroplax*. They have similar relations to the basisphenoid, parasphenoid and maxilla. There is the same row of small teeth parallel to those of the maxilla with larger teeth inside them, and the pterygoid is covered with the same shagreen of fine teeth."

Watson also states that unlike later Stegocephali *Loxomma* has a single median occipital condyle on the basioccipital, and that this condyle "exactly resembles the end of a vertebral centrum, which it no doubt is." In these features *Loxomma* therefore agrees with Rhipidistia rather than with typical Stegocephali. In reference to the dentition of *Loxomma* Watson states that:

"The Palatine is very similar to the transverse in general character, but bears two large tusks near its outer border. Each of these teeth has associated with it a shallow pit from which a tooth has been shed, and in which a replacing tooth will be formed. In some cases both teeth are present at once, a condition which was undoubtedly only transitory; this curious type of tooth change is very characteristic of the Stegocephalia, and is unknown elsewhere except in the Crossopterygian⁶ fish, where it occurs in a very typical form in the vomerine tusks of *Megalichthys*, and no doubt in many other genera, and in *Lepidosteus*. This occurrence seems to me a strong additional reason for regarding the Tetrapoda as derived from this group of fish."

The infolded base of the teeth in the Rhizodontidæ is also strongly suggestive of stegocephalian affinities, but may be only an independent adaptive device for fastening the teeth to their bases.

⁶ "Throughout this paper 'Crossopterygian' is used as including only the three families Holoptychiidae, Rhizodontidae and Osteolepidae of S. Woodward's sub-order Rhipidistia, and excluding *Tarrasius*, *Caelacanthus* and *Polypterus*." (Watson).

Although the chondrocranium of *Rhipidistia*, except for the basioccipital and basisphenoid elements, is not well known, it was probably fundamentally similar to that of *Polypterus*, and here it may be remarked also that the sphenethmoid of that fish is similar to the element of the same name in modern Amphibia, and that Broom (1913, p. 587) has recently described the sphenethmoid of the stegocephalian genus *Eryops* as recalling that of *Polypterus* in certain details.

The lower jaw of *Rhipidistia* differs considerably in form from that of *Stegocephali* and retains a full series of gular elements median, paired and lateral, as well as a row of infradentaries; certain of these elements, especially the paired gulars, seem to have been lost in the *Stegocephali*, while some others are with difficulty traceable.

In spite of these differences, however, the primitive stegocephalian jaw, as described for instance by Williston (1913), Broom (1913, p. 575) and Watson (1912, p. 11), has many important characters in common with the jaws of *Osteolepis* and *Rhizodopsis*, as described respectively by Pander, Traquair and others. Putting together the suggestions of homologies made by Smith Woodward, Watson and Broom (1913, pp. 77-78) we would have the following table:

RHIPIDISTIA	STEGOCEPHALI
First infradentary	Splénial (Woodward)
Intermediate infradentaries	Postsplénial (Watson)
Posterior two infradentaries	Angular and surangular
Dentary	Dentary
Coronoids (? "splénial" of <i>Amia</i> and <i>Polypterus</i>)	Coronoid and precoronoid
Prearticular (<i>Sauripterus</i>)	Prearticular
Articular	Articular

STEGOCEPHALI

When the classification of the dermal elements of the skull-roof which has been worked out in the preceding pages for the *Rhipidistia* is applied to the skull-roof of the *Stegocephali* the following correspondence results (*cf.* Fig. 3):

RHIPIDISTIA

STEGOCEPHALI

A. Dorsal series

1. Rostro-frontal segment

Premaxillæ	} More or less undivided	Premaxillæ	} Sharply separated
Ethmoid		Ethmoid	
Nasals		Nasals	
"Anterior frontals" (ectethmoid)		? Septomaxillary	
Frontals		Frontals	

2. Parietal segment

Parietals	Parietals
"Squamosals" (pterotics)	Pterotics ("Supratemporals", "supra-squamosals")

3. Occipito-nuchal segment

(Nuchal median "supratemporal")	Paired dermo-supraoccipitals (post-parietals)
Lateral "supratemporals"	Tabularia ("epiotics")

B. Circumorbital series

Including a variable number of elements: in <i>Holoptychiidæ</i> , <i>Glyptopomidæ</i> , three ("prefrontals", "postfrontals", "suborbitals"); in <i>Osteolepidæ</i> four or five; in <i>Rhizodontidæ</i> five	Including always five elements: prefrontal lacrymal, jugal, postorbital, postfrontal
--	--

C. Temporal-opercular series

Pterotic ("squamosal")	Pterotic (supratemporal, suprasquamosal)
Cheek plate X (= posterior postorbital of <i>Amia</i>) and true operculum	Squamosal
Cheek plate X' (interoperculum)	Quadratojugal
Operculum	? Become membranous, or transformed into tympanic membrane of <i>Stereospondyli</i>
Suboperculum	? Lost (become membranous)

The dorsal segments as above defined include only transverse zones: but, running longitudinally from the top of the orbit to the top of the occiput and external to the primitive spiracular cleft (*Polypterus*, *Holoptychius*), there is a postorbital-pterotic row which corresponds in position to the postorbitals, intertemporals and pterotics (supratemporals) of Stegocephali.

The supposed correspondence in the elements of the lower jaw between the Osteolepidæ and Rhizodontidæ on the one hand and the most primitive Stegocephali on the other have been noted above (p. 334).

According to Watson, the resemblances in the under side of the skull between *Megalichthys* and the primitive Stegocephali (*Loxomma*, etc.), which have a single occipital condyle, is remarkably close, and apparently there is little doubt as to the homology of the following elements in the two groups: premaxillæ, maxillæ, prevomers, palatopterygoids, parasphenoid, quadrates, hyomandibular (stapes), basisphenoid, basioccipital

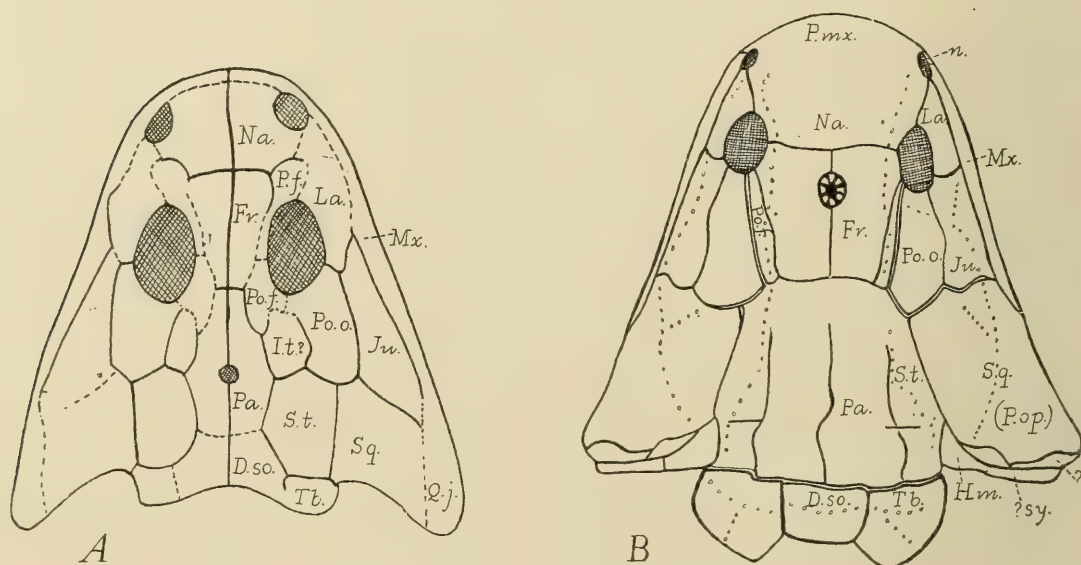


FIG. 3.—Skull patterns of *Trimerorhachis* and *Diplopterus*

A, Permo-Carboniferous stegocephalian, *Trimerorhachis medius* (order Temnospondyli), after Broom. B, Devonian osteolepid rhipidistian *Diplopterus*, after Jaekel (lettering somewhat altered).

Abbreviations as in Fig. 2, p. 330; also: *It*, intertemporal; *H.m.*, hyomandibular (columnella auris); ? *sy.*, ? symplectic (? extra columella).

In B the interfrontal foramen is identified by authors as the pineal opening. The brain was probably located far forward.

(a modified centrum). Again the elements of the chondrocranium, so far as they are known in Stegocephali (*Trimerorhachis*, *Eryops*), seem to correspond in general plan with the conditions in the existing *Polypterus*.

It is conceivable that the Stegocephali may have branched off from the stem of the Rhipidistia before the skull-roof became fully ossified, but the existence of such an extensive series of correspondences offers strong evidence of community of origin. It seems reasonable, therefore, to conclude that the primitive stegocephalian skull has been derived from the rhipidistian skull through the following advances:

1). The rostro-frontal segment has usually become more elongate and always more completely differentiated (nostrils larger, separate nasals and premaxillæ, distinct internal nares).

2). The orbits have increased in size and are generally displaced backward farther from the nares.

3). A pineal foramen between the parietals has appeared.

4). The elements of the skull-roof usually have acquired more polygonal, or angulate, and less rectangular, outlines.

5). The postorbital-pterotic series, lying above the spiracle and bearing a supraorbital sensory tract has given rise to the postorbital, intertemporal and true supratemporal (pterotic) of the Stegocephalia (cf., *Stegops divaricata* Moodie).

6). The circumorbital series have come into closer sutural relations with the surrounding elements and appear as the prefrontal, lacrymal, jugal, postorbital and postfrontal.

7). When the shoulder-girdle became freed from the skull by the atrophy of the posttemporals the median nuchal plate became firmly attached to the parietals and was divided by a median suture into the paired dermosupraoccipitals, while the lateral nuchals, also becoming attached to the parietals and pterotics, gave rise to the tabularia (epitotics).

8). The operculum and suboperculum, as well as the median paired and lateral gulars, lost their bony constituents and became membranous. This may have resulted from a complexity of changed conditions following upon the assumption of air-breathing habits, the dwindling of the branchial arches and the reduction of the cleithrum (with which in *Crossopterygii* the operculum is in close contact, see page 354). The branchial chamber may also have served more or less as a resonating chamber and sound vibrations may have been transmitted from the outer air, through the operculum and hyomandibular (stapes)- to the side of the otic capsule, so that the operculum may have given rise to the tympanic membrane of *Stereospondyli*, which had the locus of the operculum and was in contact with the squamosal (preoperculum), stapes (hyomandibular) and tabulare (lateral shoulder plate).

9). The preoperculum and interoperculum (X') covering the side and lower part of the quadrate in *Rhipidistia* did not share the fate of the operculum but gave rise to the squamosal and quadratojugal, respectively.

10). As a result of the loss of the bony character of the opercula the fossilized skull of the Stegocephali is sharply truncated behind the occiput and squamosal and in the young stages the branchial arches (cf., *Branchiosaurus*) are exposed. As the Stegocephali were almost certainly de-

rived from Osteichthyes of some sort, it is highly probable that their ancestors had fully developed nuchal, opercular and branchiostegal or gular elements, and their disappearance may be accounted for by the foregoing hypothesis.

11). The "otic notch," between the cornu of the tabulare and the squamosal, was probably not a direct inheritance from rhipidistian conditions but was progressively developed in the Stegocephali.

12). From Watson's observations on *Megalichthys* it would appear that the base of the skull was transmitted from the rhipidistian stem to the earliest Stegocephali with very little change, but in the typical Stegocephali the median occipital condyle had been largely withdrawn and the paired exoccipitals furnished the chief articular surfaces for the vertebral column, while the interpterygoid vacuity, becoming much expanded, gave rise to the well-known fenestrate palate with widely divergent pterygoids.

COMPARATIVE STUDY OF THE PECTORAL LIMBS IN PRIMITIVE FISHES AND TETRAPODA

ORIGIN AND EARLY HISTORY OF THE LOCOMOTIVE APPARATUS OF VERTEBRATES

The problem of the origin of the Tetrapoda in practice is not easy to circumscribe or isolate: for it is almost inextricably connected with other phylogenetic and morphological problems, including some of the widest scope.

After we have compared the skulls of the earliest Tetrapods with those of fishes and have adopted provisional views as to the homologies and transformations of the various elements of the skull in the two classes, we must take up the difficult problem of the origin of paired limbs of cheiropterygial type from some form of piscine appendages. But no satisfactory solution of this can be attained until the problem of the origin of fins in general, including both median and paired fins, has been attentively considered. Here we must weigh Gegenbaur's famous theory, that the median and the paired fins have had a different mode of origin, the paired fins being modified gill structures, against the opposing theory that both median and paired fins have had a similar mode of origin, from folds of skin: and after we realize the far-fetched and mystifying character of Gegenbaur's theory and the strength of the embryological and palæontological evidence in favor of the opposite theory that has been set forth by Wiedersheim (1892) and in more recent years by Goodrich, Dean, R. C. Osburn (1906) and others, we come to the further realization that paired limbs, paired fins and median fins are all purely acces-

sory locomotive structures, which transmit to the surrounding or supporting medium the thrusts of the primary and essential locomotive organs, which are the myomeres.

If in turn we inquire into the nature and origin of the myomeres we enter upon some of the master problems of vertebrate morphology, especially the origin of the mesenchyme, mesoderm and coelom, the early metamerism of the chordates and the phyletic relations of the Chordata to other phyla of Metazoa. While no one would claim that these greater problems are fully settled, yet the modern studies of Sedgwick, Lankester, Goodrich, Patten, Castle, Kingsley, Willey, Delage and Hérourard (1898) and many others, afford a strong evidential basis for some such synthetic concept of the earlier evolution of the chordates as may now be outlined.⁷

The pre-Silurian and perhaps pre-Cambrian ancestors of the Chordata were, I believe, related neither to the Arthropoda, Annelida or any other phylum exhibiting metamerism; the elaborate resemblances discerned by Patten and others between limuloid and chordate structures being regarded as the homoplastic results of similar locomotive adaptations on the part of independent phyla having in common chiefly the following characters: (*a*) anteroposterior motion, (*b*) a metameric repetition of mesodermal tissue, (*c*) a subsequent independent process of cephalogenesis or concentration of neuromeres.

Possibly these pre-Silurian chordates may have traced back their origin to the stem of the echinoderms, or they may have been coelenterates of some sort, as suggested by Sedgwick and by Masterman. Possibly they are pictured in a general way by the early larvæ of *Balanoglossus* and echinoderms. At any rate they were at first more radiate than bilateral in plan. They had a more or less ciliated epidermis, the cilia being the first locomotive organs of all known phyla. Their primitive gut or archenteron may have borne several diverticula, more or less similar to the five "archimeres" of *Balanoglossus*, which were destined to give rise to the myocoelomic pouches of chordates (Lankester). These myocoelomic pouches are thought by some to have surrounded the gonads, which were derived from the archenteron, and a primary segmentation of the gonads, corresponding to that of the myotomes, was assumed; but Kingsley states (1912, p. 319) that in the existing vertebrates no metamerism of the gonads exists. At any rate the segmental myocoelomic pouches very early came into functional relations with the gonads, through the formation of segmental nephridial ducts.

⁷ A preliminary report on this subject was read before the New York Academy of Sciences, Nov. 13, 1911. Abstract in Science N. S., vol. XXXIV, p. 892. 1911.

The steps by which the primitive radiate symmetry changed into bilateral symmetry are quite vague, but the change no doubt involved the progressive contractility of the myocœlomic pouches and the assumption by some of them of a partly locomotive function.

Bilateral symmetry was, at least, one of the earliest of all chordate acquirements and may have led the way for such fundamental characters as metamerism, a notochord and a nervous system of vertebrate type. The myocœlomic pouches very early began to increase in size and number and in power of contractility; all this accompanying an emphasis of bilaterality, a moderate lengthening of the anteroposterior axis and the assumption of an obtusely fusiform shape. The nervous elements, perhaps originally more or less diffused in the skin, were segregated in definite tracts, which foreshadowed the chordate neuron and segmental nerves. The anterior part of the gut gave off paired diverticula on either side, which may at first have served to draw in a food-bearing current of water, but later assumed a respiratory function, acquired exterior fistulæ and gave rise to the branchial apparatus of chordates. The myocœlomic sacks, extending ventrally, inclosed the primitive gut below; the cœlenterate mouth was closed and a new mouth was opened, formed from the coalescence of opposite pharyngeal diverticula. The dorsal moiety of the myocœlomic sacks gave rise to the muscle segments, the ventral moiety to the cœlom. Meanwhile the mesenchyme, which in modern vertebrates arises chiefly from the splanchnic and somatic walls of the muscle plates, was giving rise not only to the corpuscles of the blood and lymph, but also to the deeper layer of the skin (corium), the involuntary muscles and the connective tissue antecedents of cartilage and bone (Kingslev), all of which were destined to become of the utmost importance in the further development of the locomotive organs.

The notochord perhaps arose as a ciliated groove on the dorsal wall of the gut, its locomotive function being secondary. The circulatory, excretory and respiratory structures were all accessory adaptations for more rapid metabolism, following the primary change of myocœlomic pouches into locomotive organs. During these early stages there was but little differentiation of head and trunk, the pharyngeal region was large, and cephalogenesis, or fusion of neuromeres etc., was in a low stage.

A critical stage in vertebrate evolution was reached when, through the coöperation of the vascular system and of the rapidly differentiating mesenchyme, a twofold skin was substituted for the primitive ectoderm, and connective tissue began to be formed around the notochord, around the sensory capsules, beneath the skin, between the myomeres and between the gill pouches. Still later the process of ossification and calcifi-

cation not only gave rise to a more fully protective exoskeleton, but afforded more rigid bases or fulera for the attachment of the segmental muscles.

A further development of the muscular system, involving superior locomotive powers, rapidly ensued, resulting in a corresponding improvement in offensive and defensive adaptations. The primitive food habits required only that microscopic food particles be drawn into the pharynx by ciliated tracts and later by the sucking action of the branchial pouches, but these primitive habits were later abandoned for the active pursuit of larger prey. At this stage also the conditions necessary for fossilization were fulfilled, the palæontological record opens with the Silurian ostracoderms, and speculation can be replaced by recorded history.

OSTRACODERMI

The subsequent history of the head, as thus conceived, has been outlined above (pp. 318-338). The acquirement of a many-layered skin and of osseous or calcareous deposits in the exoskeleton also conditioned the formation and rapid improvement of accessory locomotive organs, especially the fins. From the beginnings of bilateral symmetry and of the differentiation of the head-end from the tail-end, there must have been a tendency for the locomotive end of the body to protrude behind the terminus of the primitive gut, and to become laterally compressed, while the tip of the head-end became either dome-shaped or depressed. In the ostracoderms the caudal end is already provided with a web of skin, serving as a sweep and strengthened dorsally by ridge scales. The form of the hard parts was everywhere conditioned by the arrangement of the underlying myomeres and their connective tissue septa, as shown clearly in the arrangement of the scales in modern fish. Dorsal, ventral and caudal outgrowths of various shapes, strengthened by hard scales or scutes, served to transmit the thrust of the myomeres to the surrounding medium.

The fusiform free-swimming Birkeniidæ while well provided with median or vertical fins were apparently not provided with horizontal or paired fins for steering up and down, this perhaps being effected by twisting the body. *Thelodus* and *Lanarkia* on the contrary were more or less ray-like in form and the lateral angle or lappet of the body may have assisted in steering up and down and in veering or dipping to one side or the other. The Cephalaspidæ had a pair of fleshy, scaly flaps behind the cephalothoracic shield, which may have been of considerable assistance in steering. In the Antiarchi the pair of lateral appendages behind the head were protected by a many-layered osseous armor, jointed so as to permit bending, and vaguely suggestive both of arthropod appendages

and of the shell-covered flippers of tortoises. A few authors have even endeavored to homologize the paired appendages of Antiarchi with the pectoral limbs of gnathostomes! Pelvic paired fins are absent in the Ostracodermi and Antiarchi, and also in the Arthrodira, as Dean (1909, pp. 282-287) has shown.

ARTHRODIRA

The exoskeleton of the Antiarchi afforded an ample base for their paired appendages as well as for the muscles of the head and thorax, and the same is true in the case of those Arthrodira which, like *Acanthaspis*, had paired spine-like appendages attached to the anteroexternal corners of their osseous plastron. Here it may be noted that the attempts of Jaekel, Tate Regan and Patten to homologize the elements of the thoracic plates of Arthrodira with the dermal plates of the shoulder-girdle of Osteichthyes appear to the present writer to constitute a begging of the question. There are, it is true, vague resemblances between the "clavicular" and other thoracic plates of Arthrodira and the pectoral plates of Osteichthyes, but in view of the amazing powers of convergent evolution, which are known by experience to many investigators, why should we assume a homology or a series of homologies and then regard them as a basis for phylogenetic speculation? The "homologies" assumed by Jaekel, Patten and Tate Regan are based merely upon a general similarity in the spatial relations of certain plates in Arthrodira and Osteichthyes with reference to assumedly homologous starting-points. Given paired orbits in the two phyla and Jaekel will call the median dorsal element lying between the orbits "frontale," the elements behind it "parietalia" and the median occipital element "occipitale superius" and assume that the so-named plates are homologous with those of Osteichthyes. And the supposed homologies of the arthrodiran shoulder plates with those of Osteichthyes are equally arbitrary and unconvincing. This matter is of some importance to our main topic, the origin of the Tetrapoda, for in Professor Jaekel's early schemes the Tetrapoda and the Placodermi were indicated as having sprung from a common pro-tetrapod stock: Patten too connects the Arthrodira with the stem of the Dipnoi and Amphibia and homologizes the pectoral plates of Dipnoi with those of Arthrodira. According to the view here adopted the Arthrodira may be an offshoot from the antiarchian stem, which "paralleled" and even surpassed the Osteichthyes in the development of the exoskeleton of the head and thorax, but failed to build up the endoskeleton to the same degree. Nor were their accessory locomotive organs (caudal fin, dorsal fin) as highly organized as in either the Elasmobranchii or the Osteichthyes.

ELASMOBRANCHII

In the earliest known elasmobranchs, the Acanthodii of the Upper Silurian and Devonian, the locomotive apparatus as a whole was in a much more advanced stage than in the typical Ostracodermi or Arthrodira. The locomotive part of the body, namely, the trunk and tail, is from three to six times as long as the cephalo-pharyngeal region and no heavy thoracic armor impedes the undulation of the fusiform body. In the earliest forms the median and paired fins are of large size and unusually numerous, for in addition to the two dorsal fins, the anal and the caudal fin, there is a whole row of accessory paired fins, or fin spines, between the pectorals or pelvics, suggesting the former presence in this region of paired ventral fin-folds. The Acanthodii are, however, definitely excluded from ancestry to the higher types, by the fact that the exoskeleton was more highly developed than the endoskeleton. The anterior borders of all the fins both median and paired were supported by fin-spines, which are believed (Dean, 1907, p. 216) to represent clusters of originally metameric dermal tubercles. Functional pectoral and pelvic girdles were also developed from dermal elements, and perhaps served for the insertion of powerful muscles, as well as for the support of the heavy spines. But the underlying cartilaginous elements were little if any developed and in my view the dermal elements of the girdles were analogous but not homologous with those of Osteichthyes. In some acanthodians (*Gyracanthus*) the pectoral fin-spines became overspecialized and attained a relatively enormous size; in other lines all the spines were reduced and the body in the later types became much elongate as in many other decadent groups of fishes (A. S. Woodward).

In brief the Acanthodii failed to carry the exoskeleton beyond a low stage of evolution, and their dermal shoulder-girdle was developed independently of that of the Osteichthyes.

The Cladoselachii avoided the line of specialization typified by the Acanthodii and indeed went to the other extreme in sacrificing a large part of the exoskeleton. But they carried much further a process which in the Acanthodii was barely begun and soon abandoned, namely, the building up and calcification of rods of cartilage, lying between the myomeres and extending out into the median and paired fins; these metameric cartilaginous rods reached almost to the tips of the fins, they were jointed at the body line and within the trunk they underwent more or less coalescence and enlargement, giving rise to the cartilaginous girdles, basals and radials. In this group the paired fins, like the median fins, had a wide base which was not exerted posteriorly from the body;

nor were the basal cartilages widely protruded. Consequently the paired fins were used rather as steering planes, which could be raised or lowered or gently undulated, rather than as paddles, capable of twisting about a narrow base.

The typical elasmobranchs have followed a conservative line in the evolution of their fins: in the distal portions of all the fins they have developed horny dermal rays or ceratotrichia, which lack a bony or calcareous basal portion, but serve well as the flexible elastic fin-web. In the typical sharks the basal cartilages have become more or less widely protruded from the body-wall, the base has shortened and the posterior border of the fin has become sharply exerted or entirely freed from the body-wall, with more or less rearrangement of the basals and radials; consequently the pectoral fins of sharks and still more of chimæroids have become very efficient paddles, capable of a wide range of movements. In the skates, on the other hand, after the primary shortening of the base and coalescence of some of the basal rods, there was a secondary antero-posterior widening of the fin, a multiplication of the radials, with dichotomization of the distal ends, and a great forward and backward extension, with corresponding emphasis of the power to undulate the outer border. The pectoral girdle accordingly becomes a stout depressed hoop and secures a firm articulation dorsally with the vertebral column. All such improvements in the median and paired fins have been accompanied by a great strengthening of the axial skeleton, and by the functional replacement of the notochord by the calcified centra, developed in and around the perichordal sheaths.

The pleuracanth sharks are of historical importance in any discussion of the early history of the paired limbs. Their pectoral limbs, recalling the "archipterygial" type of Gegenbaur, were assumed to be the most primitive form known and the vague resemblance of the pectoral girdle and fin to a gill-arch and its extrabranchial rays were by no means overlooked. But it is now coming to be realized that the pleuracanth, which are of Permocarboniferous age, were highly specialized, aberrant sharks, living in fresh-water, along with branchiosaurs, microsaur and other swamp-dwelling types, wriggling about with their long *Gymnotus*-like body or paddling with their *Ceratodus*-like pectorals. Whether the diphyccercal tail of pleuracanth is a primitive structure is doubtful. The loss of the primitive heterocercal tail and the assumption of the gephyrocercal form in *Ceratodus*, *Protopterus*, *Lepidosiren* and certain swamp-living teleosts (symbranchoids, gymnotids, gymnarchids, etc.) is an indication not of primitiveness, but, as Dollo has shown, of degenerative specialization. On the other hand the tail-fin of pleuracanth

approaches the hypothetical generalized form which Schmalhausen (1913, p. 66), after thorough studies of the musculature and skeleton of the caudal fin of fishes, regards as antecedent to the heterocercal tail of typical elasmobranchs.

That the pleuracanth is truly a shark, although of a peculiar order, is definitely proved by their skull-structure, which has been cleared up by Hussakof (1911). As for their pectoral fins, the general resemblance to those of *Ceratodus* offers an excellent example of convergent evolution: the protrusion of the metapterygial axis, perhaps followed by a process of asymmetrical budding, having resulted in both phyla in a more or less mesorhachic or biserial fin; so that we may regard this type as a "morphon" which has arisen independently in widely removed phyla. The pelvic fins of *Pleuracanthus*, and indeed of all sharks, are, according to the view here adopted, in a lower stage of evolution, since their bases are less widely protruded from the body and they have departed less from the fin-fold type.

The large and high coracoscaphular cartilage of pleuracanth remains separate from its fellow of the opposite side; in form it parallels that of Tetrapoda and supports the large pectoral limbs, which have a single proximal basal piece analogous to the humerus. If the pleuracanth had happened to develop dermal plates around the shoulder-girdle we should have had still more resemblances to *Ceratodus* and the Tetrapoda, to lead further astray investigators who neglect the "potency of convergence."

In brief the elasmobranchs show a marked advance over the ostracoderms in all locomotive adaptations. In the development of median and paired fins the earliest elasmobranchs overemphasized the exoskeleton; some of the later ones on the contrary neglected the exoskeleton (*Cladoselellachii*, pleuracanth), but developed the endoskeleton to a high stage. The basal cartilages, which were formed between the myomeres of the fins, coalesce, enlarge and are widely protruded from the body to form pectoral paddles either of tribasal, or rarely, of sub-mesorhachic type. The pelvis remains on a lower stage of evolution, retaining usually a broad base and acquiring an over-extended metapterygium.

ACTINOPTERYGII

The earliest Actinopterygii preserved that fortunate balance between endoskeletal and exoskeletal structures which, as Dr. Smith Woodward (1906) has shown, was essential for the highest development. First they either inherited or reinvented bone-cells, which, being carried to almost any desirable point by the mesenchyme and vascular system, served to reinforce the exoskeleton and to replace the cartilaginous endoskeleton.

The Actinopterygii also introduced several other important improvements in the accessory locomotive structures. In the exoskeleton they avoided overspecialization of the outermost layers, a *cul-de-sac* into which the elasmobranchs entered, and while at first developing in due proportion the ganoine, cosmine, vasodentine and isopedine strata, they avoided the errors of the typical ostracoderms and antiarchians and did not cumber themselves with a massive carapace and plastron.

In the median and paired fins they were fortunate in evolving a type of rod-like scales, which by fusing end to end, gave rise to the dermal rays; these soon became the most important part of all the fin-web and entirely superseded the horny fin-rays of an earlier period. With the advent of these superior fin-rays and with the concomitant strengthening of the vertebral column by neural and hæmal rods, and finally by ossified centra, the caudal fin in the Actinopterygii became of predominant functional importance and changed from the heterocercal to the homocercal type, receiving the powerful thrusts of the myomeres, which were transmitted to it along the reinforced vertebral column. The hæmal rods below the caudal column served to link the tail to the backbone. At first they were slender and numerous, but gradually were reduced in number and expanded into the broad hypural bones, around which the stout dermal rays were tightly clamped.

In the later Actinopterygii the body frequently became elongate, the paired dorsal and anal fins were reduced, the dermal rays became reduced, and the once powerful caudal degenerated into the pointed gephyrocercal type. The varied history of scales and dermal rays of the Actinopterygii illustrates the comparative rapidity with which these structures change or disappear. The forerunners of the group may well have had scales like those of the most primitive crossopterygians and dipnoans; but even in the Palæoniscidæ the ganoine has become many-layered and the cosmine layer is modified. In later Actinopterygii the ganoine and cosmine disappear, the scales sink beneath the skin, lose their osseous tissue and become horny.

The over-development of the lepidotrichs or dermal rays may perhaps be responsible for the failure of the Actinopterygii to attain the highest development of the endoskeleton of the median and paired fins. In the earliest form (*Cheirolepis*) as restored by Smith Woodward the pelvic fin had a very extended base with short rod-like basals and radials, the pectoral fin had a shorter base, which was, however, wider than that of later types; the dermal rays were long, numerous and scale-like. With the collapse of the archipterygial theory there is no longer any reason why this wide-based type of fin that occurs so near the beginning of the

record, should be regarded as a highly modified archipterygium, especially as the paired fins are identical in plan with the vertical fins. And yet some authors (*e. g.* Braus, 1901) have assumed that the paired fins of *Amia*, a much later and more specialized actinopterygian than *Cheirolepis*, were of reduced archipterygian type. The point is important in relation to the origin of the Tetrapoda, for if the early Actinopterygii ever passed through an archipterygian stage they might be more closely related to the Tetrapoda than is generally admitted. But none of the

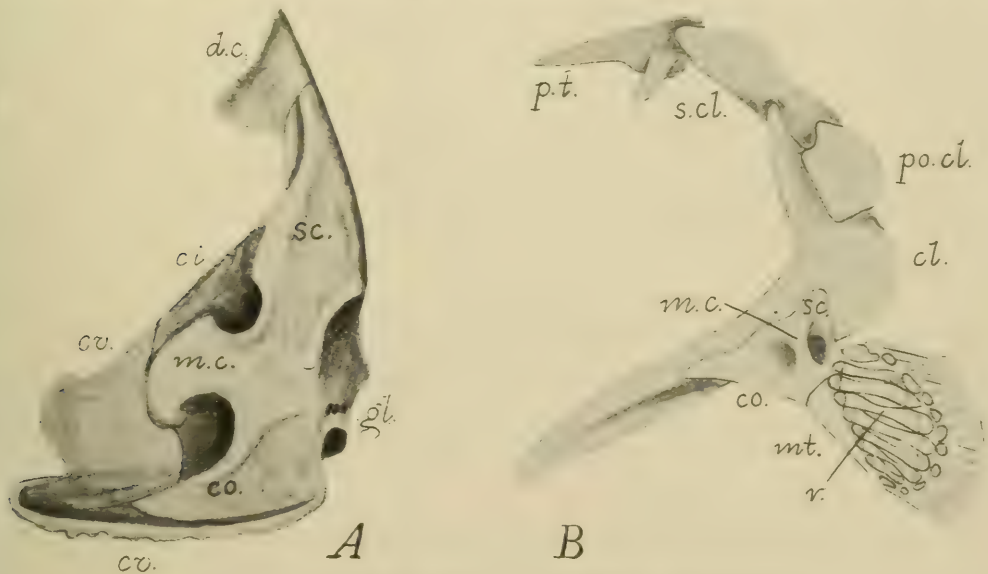


FIG. 4.—Pectoral girdle of *Acipenser* and *Amia*

(A) *Acipenser sturio*, after Goodrich, from Gegenbaur. (B) *Amia calva*, from Goodrich. Inner (medial) view of right side.

Dermal elements: *cv*, clavicle ("infraclavicle"); *cl*, cleithrum ("clavicle"); *s.cl*, supraclathrum; *p.t*, posttemporal; *po.cl*, postcleithrum.

Cartilage elements: *co*, coracoid; *m.c*, mesocoracoid; *gl*, articular surface; *sc*, scapula; *d.c*, dorsal cartilage.

The sturgeons have the largest coracoscapula of any Actinopterygii: it is unossified; the true clavicles are present and of large size. In *Amia*, as in more typical Actinopterygii, the coracoscapula mass is of relatively small size, this corresponding with the relatively small size of the fin-muscles; the coracoscapula is more or less ossified and suturally divided into dorsal and ventral moieties named scapula and coracoid, respectively; the true clavicles have disappeared, and the cleithrum is connected with the skull by the stout supraclathrum and forked posttemporal.

early Actinopterygii show the least visible trace of ever having had widely protruded basal elements in the paired or median fins: on the contrary they emphasized the dermal rays and an undulatory movement of the margins of the fin, rather than of its fleshy base.

In the shoulder-girdle (Fig. 4) the Actinopterygii also developed the dermal elements rather than the cartilaginous endoskeleton, the sturgeons and their allies being the only ones with a large coracoscapula cartilage (Fig. 4A). In most Actinopterygii the coracoscapula cartilage is small

(Fig. 4B), while the dermal elements of the shoulder-girdle (except the true clavicles which disappear) are fully developed. These dermal elements are associated with the opercular and branchiostegal series and serve to attach the pectoral girdle to the skull; but their chief function is to serve as a base for the coracoscapula, which bears the principal muscles of the fin. The homology of all these elements with those of the Tetrapoda is discussed below.

In brief the typical Actinopterygii while progressively emphasizing the bony tissue, both in the exoskeleton and the endoskeleton, enjoyed only a moderate development of the basals and radials of the paired fins, never protruded the basal elements widely from the body-wall and depended primitively on the caudal fin as the chief accessory locomotive structure, originally using the other fins chiefly as keels, rudders, brakes and balancers (R. C. Osburn, 1906).

DIPNOI

In this group the exoskeleton is primitively like that of the earliest Crossopterygii, but it soon undergoes degenerative changes (Goodrich, 1909, pp. 230, 238) sinking beneath the skin and losing the ganoine and cosmine layers. The endoskeleton, on the other hand, never passes beyond the cartilaginous stage.

The earliest Dipnoi resemble their contemporaries the Rhipidistia in having two dorsal fins, a heterocercal tail, lepidotrichia with ganoine and cosmine, and paired fins of mesorhachic or biserial type.

The tail never attains the homocercal type; it never attains much-expanded hypurals, but passes from the primitive heterocercal type through intermediate stages, described by Dollo (1895), into the degenerate gephyrocercal. In such an animal the caudal fin has not the commanding functional importance that it has in the typical Actinopterygii, and there is a very evident tendency to throw the function of locomotion more upon the paired fins and upon an eel-like undulation of the body. The Dipnoi parallel the recent Amphibia in this respect and the more specialized types also show a reduction of the dermal rays. The paired fins of the Devonian Dipnoi and still more of the modern *Ceratodus* are externally very unlike the paired fins of elasmobranchs or Actinopterygii; they also resemble vaguely the paddles of plesiosaurs rather than the cheiroptergia of tetrapods. The modern *Protopterus*, however, sometimes uses its pectoral and pelvic fins as if they were legs, crawling about, while floating in the water, on the tips of them (Dean, 1903); while *Ceratodus* sometimes rests in the water (Dean, 1906), with the tips of the pectorals turned downward and touching the bottom. But the ability

to do this ranks very far below the ability to support the weight of the body on the paired limbs without the buoyant effect of the water, as in the Tetrapoda.

In *Ceratodus* the preaxial or upper border of the pectoral fins is believed to be serially homologous with the ventral border of the pelvics. Braus (1901, p. 165) states that the earliest anlage of both fins are horizontal, that the nerve entrance of the pectoral is on the lower, or ventral, surface, while that of the pelvic is on the dorsal surface. According to this view the preaxial border of the pectoral has been rotated upward as in most Actinopterygii while in the pelvics the preaxial border has been rotated downward. Schneider (1886, quoted by Howes, 1887, p. 12) held that "die Seitenstrahlen der dorsalen und ventralen Hälfte der [pectoral and pelvic] Flossen sind ungleich," and that the "Seitenstrahlen der dorsalen Hälfte der einen Flosse entsprechen derjenigen der ventralen Hälfte der anderen." Goodrich (1909, p. 244) says that "when at rest the preaxial margin of the pectoral fin is borne upward; the reverse is the case with the pelvic fin." But Howes (1887, pl. II) has described a pelvic fin of *Ceratodus* in which this reversal has not been effected and he records so many irregularities in the structure of both pectoral and pelvic fins that the condition of reversed homology seems to be incompletely attained.

Many investigators (*cf.* Keith, 1912, p. 418) have sought to show that in man there is a somewhat similar condition of reversed homology in the borders of the pectoral and pelvic extremities; but according to H. H. Wilder (1909, p. 245), the evidence of embryological history as well as of comparative anatomy lends strong support to the opposite view that in the Tetrapoda the preaxial or anterior border of the pectoral extremity is homologous with the preaxial border of the pelvic extremity, a conclusion which is further strengthened by the general correspondence in the arrangements of the elements of the manus and pes in the most primitive Tetrapoda of the Permocarboniferous, such as *Eryops*, *Stereosternum* and the cotylosaurs.

If the latter view be correct the reversed homology of the borders of the pectoral and pelvic fins in *Ceratodus* is a point of marked difference from the Tetrapoda, which may have been acquired only by the later Dipnoi.

As the paired fins of even the oldest Dipnoi are already biserial in form, there is no direct palæontological evidence as to their origin. In the allied group of Rhipidistia, however, we get several hints as to the origin of the "archipterygial" type. *Osteolepis*, which I regard as the most primitive member of the group, on account of its skull structure,

rhombic scales and heterocercal tail, has a short wide fleshy lobe in the pectorals while the pelvics according to Traquair's restoration (Goodrich, 1909, p. 283) have still shorter and relatively wider lobes. Thus the pelvics in turn are only a little more advanced than the anal and posterior dorsal. In *Glyptopomus* the pelvic base is narrower and the axis more protruded, but the resemblance to the widely based dorsal and anal fins is still obvious. But the pectoral of this genus has become almost fully archipterygial. Coming to the Dipnoi, in *Dipterus* the process is carried further and the resemblance between the pelvic and the anal is progressively effaced. In the latter Dipnoi the "archipterygium" is perfected by the protrusion of the mesopterygial axis to the extreme tip of the fins; the pelvic fin also is finally as fully developed as the pectoral.

Turning to the evidence of comparative anatomy we find that in *Ceratodus* the plexuses of nerves that supply the pectoral and pelvic fins are brought together by the coalescence of many segmental nerves (Braus, 1901) and by analogy with the conditions in sharks (*cf.* Goodrich, 1909, pp. 72, 78), where both the paired and median fins are formed in the same manner, through the concrescence of myotomic elements, it appears highly probable that in *Ceratodus* also the narrow-based fins arose through the concentration of metameric elements, the base becoming constricted, as the power of rotating the fin increased. From the cone-in-cone arrangement of the myomeres of the *Ceratodus* paired fins it seems also probable that the outgrowth of the mesopterygial axis to the very tip of the fin was due to a sort of apical budding, or repetition of similar segments, on the part of the mesopterygium and its radials. That the central axis of the *Ceratodus* fins does represent an outgrowth of the mesopterygium was held by Huxley in opposition to Gegenbaur, and was supported, with strong evidence, by Howes (1887).

From these and similar considerations I reject the traditional view that the "archipterygia" of Dipnoi are primitive structures and I regard the imperfect archipterygia of the Devonian *Osteolepis* as more primitive than the perfected archipterygia of the modern *Ceratodus*. Nor can I accept the views of Watson, Smith Woodward and others that the paired limbs of the Rhipidistia are "reduced archipterygia"; they seem rather to be incompletely evolved or primitive "archipterygia," with less extended mesopterygia and an asymmetrical arrangement of the radials (parameres), those on the postaxial border being fully developed, the preaxial parameres being small or wanting.

The pectoral and pelvic fins of existing dipnoans have this important character in common with the paired limbs of Tetrapoda, namely, that

the endoskeletal base consists of a single proximal element, analogous respectively with the humerus and femur. Other proposed homologies of the more distal elements with the forearm, carpus and digits have been assumed, but lack adequate evidential support.

The shoulder-girdle of the Devonian Dipnoi evidently included dermal elements ("infraclavicles," "clavicles," etc.) and underlying cartilaginous elements, which, as Smith Woodward says (1898, p. 63), "seem to have been always too slightly calcified for preservation." But from the resemblance of the pectoral limb of *Dipterus* to that of *Ceratodus*, it is highly probable that the endoskeletal elements in the Devonian forms were fundamentally similar to that of *Ceratodus*.

The accompanying figures (Fig. 5), drawn from a specimen of *Ceratodus forsteri* by Professor L. A. Adams, show that in the modern genus the chief cartilaginous element, which is supposed to be homologous with the coracoscapula of the Tetrapoda, is of large size, and includes a short ascending ramus corresponding to the scapula, a tripartite, protuberant articular pedicle, and a long forward-and-inwardly projecting coracoid. This undivided element is firmly adherent to the antero-internal surface of the conjoined dermal elements first named by Gegenbaur clavicle ("infraclavicle" of early writers) and cleithrum ("clavicle"). A small median ventral cartilage (*m. v. c.*) unites the opposite clavicles, while a broad dermal supracleithrum connects the pectoral girdle with the post-temporal.

This shoulder-girdle is apparently more primitive than that of the primitive Tetrapoda in the slight dorsal extension of the scapula, in the unexpanded form of the coracoid, and especially in the protuberant form of the articular region; also, there are no centers of ossification tending to divide the coracoscapula mass into distinct elements. The dermal elements, especially the cleithrum and supracleithrum, are of large size, whereas in Tetrapoda they are much reduced. This shoulder-girdle is on the whole nearer to the tetrapod type than that of any other existing fish.

The pelvic girdle of *Ceratodus* also differs from that of typical fishes and approaches that of the primitive Tetrapoda in having a stout cartilaginous base, perhaps homologous with the ischio-pubis. The "pre-pubic" and "epipubic" processes are of doubtful homology. No dorsal process analogous with the ilia and extending up from the acetabulum toward the backbone is present.

In brief the more specialized Dipnoi have paralleled the urodele Amphibia in the reduction of the dermal rays, in the degeneration of the scales, in the non-development of a powerful homocercal tail, and in the

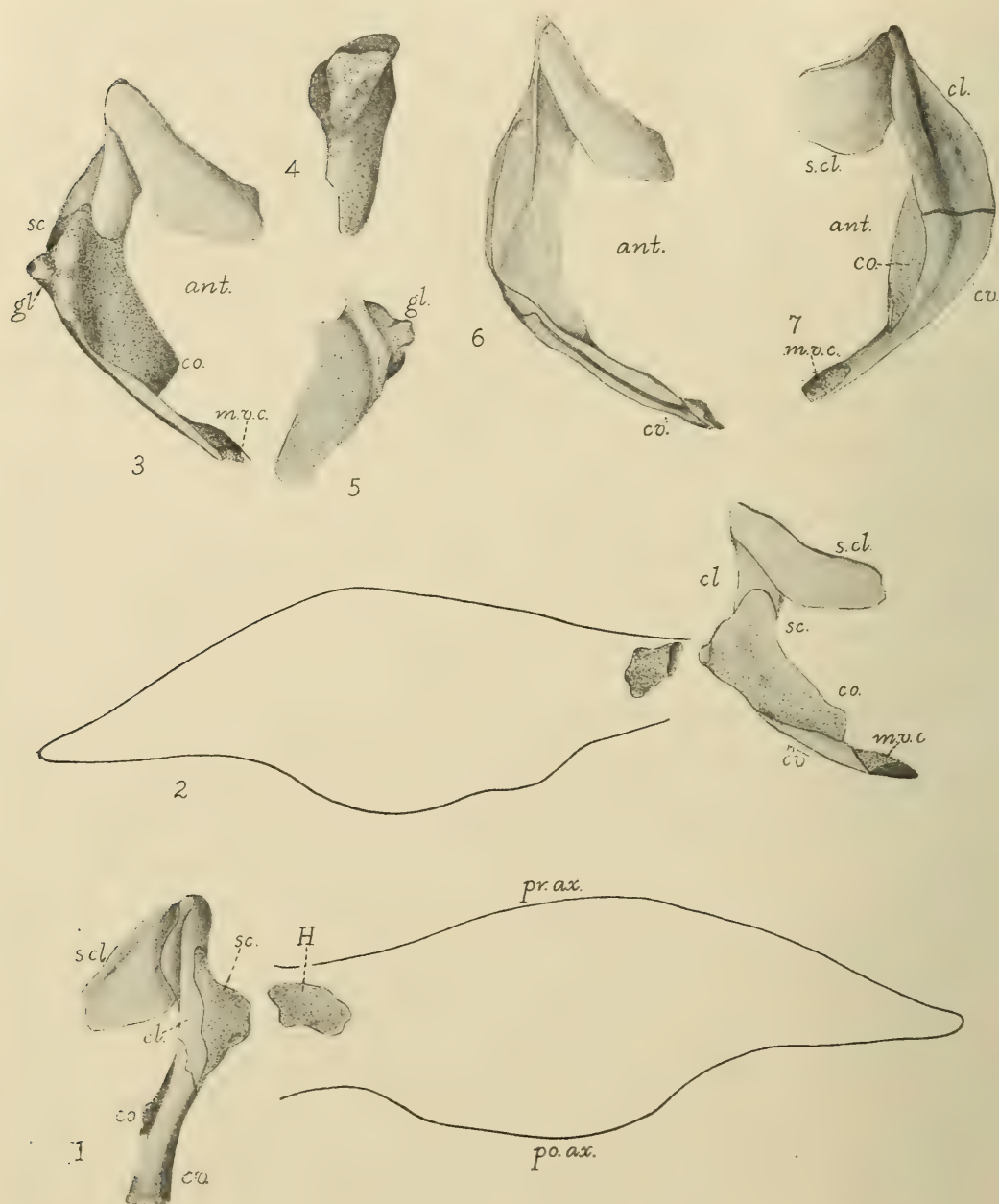


FIG. 5.—Pectoral girdle and fin of *Ceratodus forsteri*

1, Left half of girdle, with fin: outer side seen somewhat from below, showing cartilaginous (stippled) and dermal elements; 2, inner side; 3, posteroventral view, showing left coracoscaphula and articular surface for pectoral fin; 4, posteroventral view after removal of coracoscaphula; 5, front outer view; 6, rear view of left coracoscaphula cartilage; 7, outer side of same, with articular surface for cleithrum (*cf.* no. 1).

Dermal elements: *cv*, clavicle; *cl*, cleithrum; *s.cl*, supracleithrum.

Cartilaginous elements: *co.sc*, coracoscaphula; *m.v.c*, median ventral cartilage; *gl*, articular surface for "humerus"; *H*, "humerus" (proximal basal).

pr.ax, preaxial or dorsal border; *po.ax*, postaxial or ventral border.

Unlike that of the Tetrapoda, the stout coracoscaphula cartilage has a very short ascending ramus; the glenoid region is widely protruded and the muscles are better developed on the visceral or internal surface.

assumption of an eel-like habitus. On the other hand the pectoral and pelvic girdles of the more primitive Dipnoi appear to preserve certain characters which may be truly homologous with those of the ancestral Tetrapoda. The "archipterygia" of Dipnoi are primitive only in name, although evolved in their essential features at an early epoch. That such "archipterygia" are ancestral to the cheiropterygia of tetrapods is unproved and rather unlikely. The single proximal basal pieces of the paired fins may possibly, however, be homologous with the humerus and radius respectively; although it is quite conceivable that here too the resemblances may be only homoplastic and due to similar concrescence of several originally separate basal pieces.

CROSSOPTERYGII

The existing *Polypterus* has no doubt departed widely from the primitive Devonian Crossopterygii, both in the exoskeleton and in the endoskeleton and has paralleled the Actinopterygii in many respects. Among its progressive characters may be noted: the replacement of the notochord by ossified centra, the development of osseous neural and hæmal arches and hypural bones (the latter, however, being arrested in development), the reduction and ossification of the coracoscapula and its division into two elements (Fig. 6), the reduction of the radials and basals, the fusion of the basals of the pelvic fins to form a pelvis, which is ossified. And *Polypterus* has also become highly ichthyized in the brain and many other characters of the soft anatomy. Among its peculiar or aberrant specializations are to be reckoned the gephyrocercal tail, the subdivided dorsal and the multiplication of the radials in the pectoral fin.

The proximal elements of the pectoral fin are often compared with the pro-, meso- and metapterygia of sharks; the so-called "pro-" and "metapterygium" forming a V-shaped articulation with the scapulo-coracoid; the ovoid "mesopterygium" lying in the middle of the fleshy lobe of the fin; but this arrangement may rather represent a modification of the *Eusthenopteron* and *Sauripterus* type of fin described below. Possibly the "metapterygium" and "propterygium" may be homologous with the radius and ulna of *Sauripterus*; the fused "mesopterygium" may represent the fused mass of radials, or parameres, which in *Sauripterus* converge toward the central axis. The single proximal piece (true mesopterygium of *Sauripterus*) in *Polypterus* has either been lost or has perhaps fused with the coracoscapula. Indeed the whole coracoscapula in the larval *Polypterus* (cf. Goodrich, 1909, p. 296) bears a puzzling resemblance to the humerus of *Sauripterus*.

At any rate the pectoral of *Polypterus* is further removed from the

primitive cheiropterygium than is the pectoral of *Sauripterus*. Klaatsch (1896) would derive the cheiropterygium of Amphibia from the crossopterygium of *Polypterus*, but the lack of a single basal piece or humerus, as well as the secondary multiplication of the distal radials, are aberrant specializations. However the pectoral of *Polypterus* does suggest the tetrapod type in this respect: that, as Klaatsch and Budgett have shown, it can be turned downward almost like a hand, so that the larval fish sometimes rests on the palmar surface of the dermal rays; the pectoral

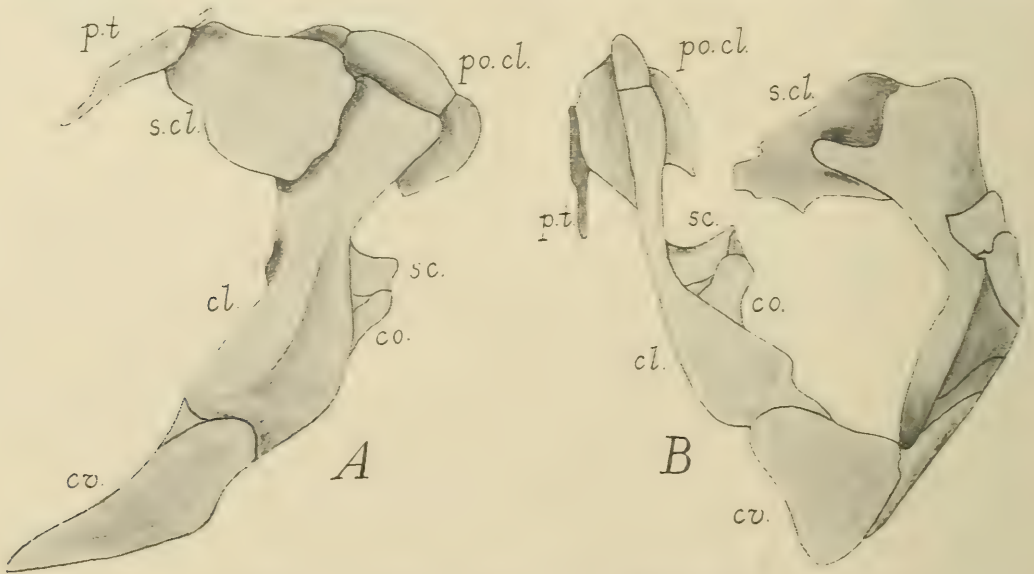


FIG. 6.—Pectoral girdle of *Polypterus bichir*

A, Left side, outer view. B, Posteroventral view.

Dermal elements: *cv*, clavicle; *cl*, cleithrum; *s.cl*, supracleithrum; *po.cl*, postcleithrum; *p.t*, posttemporal.

Cartilaginous elements: *co*, coracoid; *sc*, scapula.

This modern fish retains the true clavicles of the Devonian crossopterygians and tetrapods. Its scapulocoracoid, however, parallels that of more typical fishes and affords a short, wide base for muscles that raise and lower the fin. The forked posttemporal and wide supracleithrum serve to connect the girdle with the skull; while the marked concavity of the whole anterior margin of the girdle denotes the presence of a large operculum and large branchial arches.

is also well provided with muscles for elevating, depressing, protracting, retracting, abducting, adducting and twisting the fin (Klaatsch, Braus).

Before considering the relationship of the Rhipidistia to the Tetrapoda it is necessary to decide which is the most primitive family, and what has been the trend of evolution within the group. Smith Woodward (1898, pp. 71-80), perhaps influenced partly by the view that the "archipterygial" type of fin is primitive, seems to have regarded the Holoptychiidae as having the most primitive paired fins, and the Rhizodontidae as more progressive in the "abbreviation" of the paired fins. "Through *Rhizodopsis* and *Gyroptychius*," he said (p. 77), "the Rhizo-

dontidæ pass almost imperceptibly into the Osteolepidæ, which have rhombic scales and usually exhibit the fusion of the bones in the frontal portion of the skull and in the mandible." Goodrich (1909, p. 285), on the other hand, places the Holoptychiidæ and the allied Glyptopomidæ first, the Osteolepidæ next, the Rhizodontidæ third and the Onychodontidæ last. He says (p. 285): "It is evident from the structure of the paired fins that the Rhizodonts differ considerably from the previous three families [Holoptychiidæ, Glyptopomidæ, Osteolepidæ], and they should perhaps not be included in the same order."

The Osteolepidæ present the following assemblage of characters which in view of all that has been said above I must regard as primitive.

- 1). Their paired fins are obtusely lobate, *i. e.*, incompletely "archipterygial" and less different from the median fins, in contrast to the extremely acute "archipterygial" fins of Holoptychiidæ.
- 2). The scales are rhombic, like those of the earliest Actinopterygii, and they retain the fully developed ganoine and cosmine layers, which are progressively lost in the Rhizodontidæ and highly modified in the Holoptychiidæ (*cf.* Goodrich, 1909, pp. 217, 285).
- 3). In the Osteolepidæ the dermal rays of the median and paired fins are less produced than in the Rhizodontidæ.
- 4). The caudal fin in *Osteolepis* is of a primitive heterocercal type, whereas in Rhizodontidæ it externally approaches the homocercal type (through *Gyroptychius*).
- 5). *Osteolepis* had a persistent unconstricted notochord without ossified centra, but the larger and more progressive members of both families (*Megalichthys*, *Eusthenopteron*) had ring centra.
- 6). As to the rostrum of *Osteolepis* representing a "fusion" of elements I have given reasons above (p. 327) for the contrary view that the nasals, dermethmoids and other elements had not yet been divided by sutures.

In brief *Osteolepis* appears to offer an ideal stem form for several phyla. One line with progressively cycloidal scales and intermediate characters of the skull-top seems to have led through *Gyroptychius* (figured by Pander, 1860, Tab. 6, 7) to *Tristichopterus* (Traquair, 1875, pl. XXXII) and *Eusthenopteron* (Hussakof, 1912, Fig. 2). Another line, preserving the rhombic scales, perhaps passed through *Diplopterus* (Pander, 1860, Tab. 4) and culminated in *Megalichthys* (Wellburn, 1900, pl. XIII; *cf.* our Fig. 7). The skull of *Rhizodopsis*, as figured by Traquair (1881, Figs. 1, 2) seems to be allied in pattern to that of *Megalichthys*, as figured by Wellburn (1900, pl. XV) and yet the former is referred to the Rhizodontidæ, the latter to the Osteolepidæ: and there are other indications that these two families are very closely allied.

In the Holoptychiidæ the scales have become large, fully cycloid and deeply overlapping and have the cosmine layer sculptured, but the Glypto-

pomidae offer a transitional stage leading back to the simple rhombic type, since in them the scales, although sculptured, are more or less rhomboidal and overlap but slightly. The Holoptychiidae moreover have excessively specialized dentrodont teeth.

The Osteolepidae and Rhizodontidae are pike-like fishes (Fig. 7), with elongate bodies and powerful caudal, dorsal and anal fins, which they may have used both in sudden rushes at their prey and in holding themselves still.

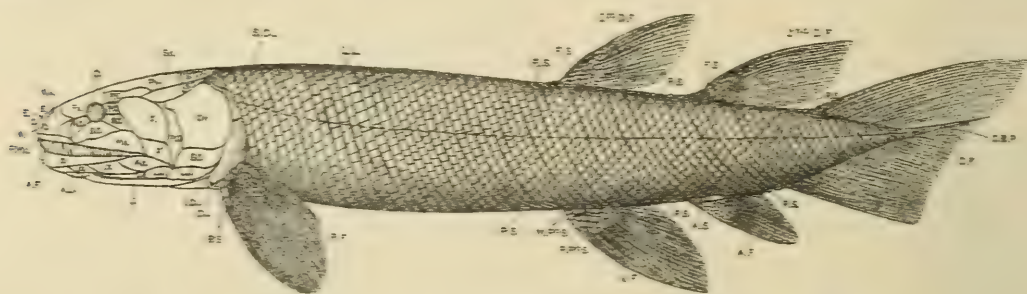


FIG. 7.—*Restoration of Megalichthys. After E. D. Wellburn*

A progressive osteolepid rhipidistian of the Coal Measures.

Skull-roof: *E.*, ethmoid; *No.*, nasal; *N.*, nostril; *AF*, "anterior frontal" [ectethmoid, septomaxillary]; *Fv*, frontal; *PF*, postfrontal; *Pa.*, parietal; *ST, ST*, "supratemporals" [dermosupraoccipital, tabulare].

Orbital series: *AO*, "anterior orbital" [lacrymal]; *SO, SO*, "suborbitals" [jugal]; *PO*, postorbital.

Temporal series: *X*, "cheek plate" [anterior portion of true squamosal]; *X'*, "cheek plate" [quadratojugal]; *SQ*, "squamosal" [supratemporal, pterotic]; *P.O.*, preoperculum [posterior portion of true squamosal].

Opercular series: *Op*, operculum; *So*, suboperculum.

Gular series: *Lj, Lj*, lateral jugular [lateral gulars]; the antero-lateral gulars may perhaps give rise to the angulare of Tetrapoda; *J*, gular; *Aj*, "anterior jugular" median gular.

Gnathal series: *Pms*, premaxillary; *Ma*, maxillary; *D*, dentary; *ID, ID*, infradentaries [splenial, preangular]; *AG*, angular [? supraangular].

Shoulder girdle: *ICl*, "infraclavicular" [clavicle]; *Cl*, "clavicle" [cleithrum]; *SCL*, "supraclavicle" [supracleithrum].

Fins: *B.S.*, basal scales; *RS*, ridge scales; *FS*, fuleral scales; *P.Pt S*, propterygial scales; *M.Pt S*, metapterygial scales; *AS*, anal scales.

Adaptation to predatory habits is indicated by the wide gape and strong sharp teeth, and by the pike-like body, with powerful median and pelvic fins, which are placed near the posterior end. The broad, stout pectoral fins would be useful chiefly in suddenly checking a forward rush and turning the head.

The Holoptychiidae on the contrary were relatively deep-bodied, carp-like forms, with weaker, longer and more flexible fins. The related Glyptopomidae were more primitive in having rhombic scales and were pike-like in form, with powerful caudal, dorsals, anals and pelvics.

What were the habits and form of the common ancestors of all these families? Probably they were comparatively short-bodied forms, with small granular rhombic cosmoid scales, two dorsal fins, a heterocercal caudal, short lobate pectorals and barely lobate pelvics; the lepidotrichs

of all fins were short and scale-like; the teeth were conical, but of small size. In general appearance, except for the shorter body, these primitive Rhipidistia may have been similar to *Osteolepis*.

Tarrasius problematicus Traquair (1881, 1890) from the Lower Carboniferous of Scotland is usually referred to the Crossopterygii and placed before the Rhipidistia in a separate order or suborder Haplistia. It is a very small fish (about 3 inches long) with a continuous dorso-caudo-anal fin and obtusely lobate pectorals; at least the posterior part of the body is covered with small granular rhombic scales; the anterior region of the trunk may have been naked; the notochord is persistent; there are neural and hæmal arches; the median fins are supported by rods, which are more numerous than the vertebral arches. *Tarrasius* was provisionally referred by Zittel to the Dipnoi, but Traquair (1890, p. 494) said that "the obtusely lobate character of the pectoral fin seems to point toward the Crossopterygii." Goodrich (1909, p. 284) states that the "dermal bones of the skull and operculum appear on the whole to resemble those of Osteolepids."

The interest of this fish in the present connection lies in its continuous median fin. By the upholders of the "fin-fold" theory it is assumed that ancestral fishes once had both the paired and the median fins continuous. But in the Actinopterygii continuous median fins are invariably a sign of aberrant specialization; and the frequently copied reconstruction of a long-bodied "primitive" fish with a continuous fin-fold bears a suspicious resemblance to such highly specialized types as *Fierasfer*, *Muraena* or *Gymnotus*. *Tarrasius* may or may not be a crossopterygian; but I find no evidence for believing that its continuous dorsal became subdivided into the two dorsals of Rhipidistia.

The point is that while paired fins and median fins probably arose in the same way, they may well have been purely local outgrowths like the dorsal fin of ostracoderms. It is not necessary to conclude that the two dorsal fins of Rhipidistia and the single dorsal fin of primitive Actinopterygii arose by subdivision or abbreviation of an originally continuous dorso-anal fin. The Actinopterygii, Rhipidistia and Dipnoi may well represent parallel offshoots from primitive short-bodied gnathostomes that had no continuous dorso-anal fin at all, but only low outgrowths of the skin or of the body-wall, placed at nodal points of mechanical advantage in securing a "purchase" against the water.

Tarrasius problematicus is also of special interest because, if it is a primitive crossopterygian, it may also be related to the stem of the Tetrapoda, retaining perhaps the lobate fins that gave rise to the cheiropterygia, retaining in part a primitive granular scalation, and developing

a diphycceral tail without powerful rays, such as might be found in an ancestor of the branchiosaurs.

The endoskeleton of the pectoral limb of the Rhipidistia offers the only remote approach to the tetrapod type hitherto known among recent or fossil types. As far back as 1843 James Hall described the pectoral limb of a large fish from the Catskill formation (Upper Devonian) of Blossburgh, Pennsylvania, and named it *Sauripterus* in allusion to the "sauroid" form of the limb. In 1908 my colleague Dr. Hussakof published a small photograph of this specimen in his Catalogue of Types and Figured Specimens of Fossil Vertebrates in the American Museum of Natural History, Part I, Fishes (p. 59). As I had long been particularly interested in the problem of the origin of the Tetrapoda I was impressed by the almost stegocephalian "look" of the pectoral limb of *Sauripterus*, and in February, 1911, I read a paper before the New York Academy of Sciences entitled "The Limbs of Eryops and the Origin of Paired Limbs from Fins" (1911) in which I proposed to homologize the ascending blade of the shoulder-girdle of *Sauripterus* with the scapulocoracoid of *Eryops*, the single basal element of the fin with the humerus, the two following elements with the radius and ulna and the remaining osseous pieces with the carpus and digits. In September, 1912, my friend Dr. Bertram G. Smith (1912, pp. 540-547) prefaced his excellent discussion of the phylogeny of the urodeles with a summary of my Columbia University lectures on the origin of the Amphibia, in which a *Sauripterus*-like type of pectoral was assumed as the starting point for the cheiropterygium; a sketch of the *Sauripterus* pectoral, by Dr. Hussakof, served to illustrate the subject. In the same year, Professor Patten, in his book "The Evolution of the Vertebrates and their Kin" (p. 390), reproduced a photograph of an excellently preserved pectoral limb of *Eusthenopteron* (Fig. 8) and said: "Within the pectoral fins, for the first time in the phylogeny of the vertebrates, appears an axial skeleton that approaches, in the arrangement of its elements, the characteristic structure of the appendages of the land vertebrates, *i. e.*, *Eusthenopteron*." In his diagram he homologized the various elements of the fin with the humerus, radius, ulna, carpus, metacarpus and digits, in much the same way as I had done in the case of *Sauripterus*. Early in 1913, Mr. D. M. S. Watson published in the *Anatomischer Anzeiger* a note "On the Primitive Tetrapod Limb" in which he also took the *Eusthenopteron* pectoral as a starting point for the cheiropterygium and regarded it as a "reduced archipterygium." In September, 1913, Dr. Broom in his paper "On the Origin of the Cheiropterygium" gave sketches of the pectoral paddles of *Eusthenopteron* and *Sauripterus* and of the shoulder-girdle of the

latter; he called attention to the resemblances in the teeth between *Sauripterus* and *Rhizodopsis* and put forth the hypothesis that the cheiropterygium had been evolved from the preaxial part of a pre-*Sauripterus* fin. Later in the same year (1913) Dr. Broom published in the *Anatomischer Anzeiger* a partial restoration of the shoulder-girdle

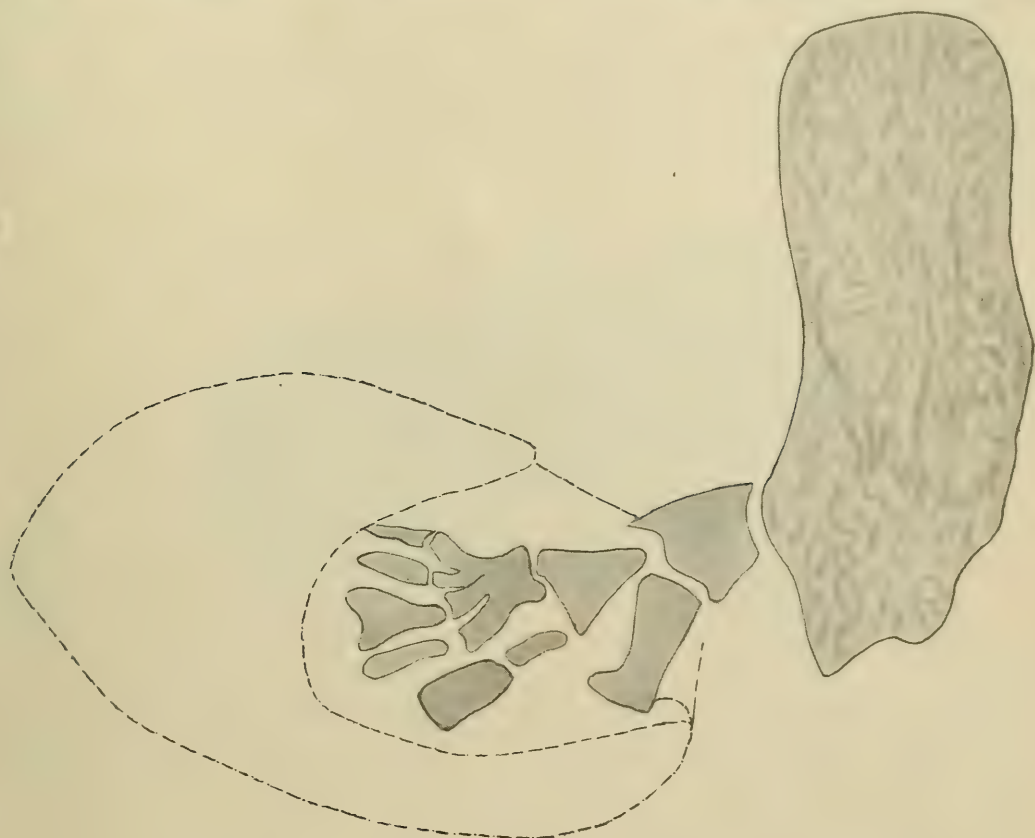


FIG. 8.—Right pectoral limb of *Eusthenopteron foordi*. After Patten

A Carboniferous rhizodont rhipidistian.

The broad ascending blade is the cleithrum; the single proximal piece was compared by Professor Patten with the tetrapod humerus, the next two elements with the radius and ulna, and the more distal elements with the carpus and digits, respectively.

The single proximal piece (humerus) probably represents the mesopterygium of sharks: together with the central line of pieces it appears to be homologous with the mesaxial series in *Ceratodus*; the divergent rods above and below this axis represent the pre- and post-axial radials, respectively. The lower main branch is the metapterygium.

and bones of the pectoral paddle of *Sauripterus* together with a sketch of the back part of the jaw.

With the view of testing my first idea that the ascending blade of the *Sauripterus* shoulder-girdle is the homologue of the scapula of tetrapods notwithstanding its dermal origin, I have studied the pectoral limb in various fossil and recent fishes and amphibians. Through the kindness of Mr. Grimshaw of the Royal Scottish Museum of Edinburgh I was

permitted to examine the specimens of *Megalichthys hibbertii* and other Rhipidistia in that Museum, while in the American Museum I have had excellent specimens of *Osteolepis*, *Megalichthys nitidus*, *Sauripterus* and much other recent and fossil material.

In view of the importance of the types specimen of *Sauripterus taylori* Hall and of the fact that it has never before been adequately figured, I have carefully studied this specimen, with the collaboration of my friend Professor L. A. Adams, whose drawing is here reproduced (Plate I). In this drawing we have endeavored to show only the structural details that

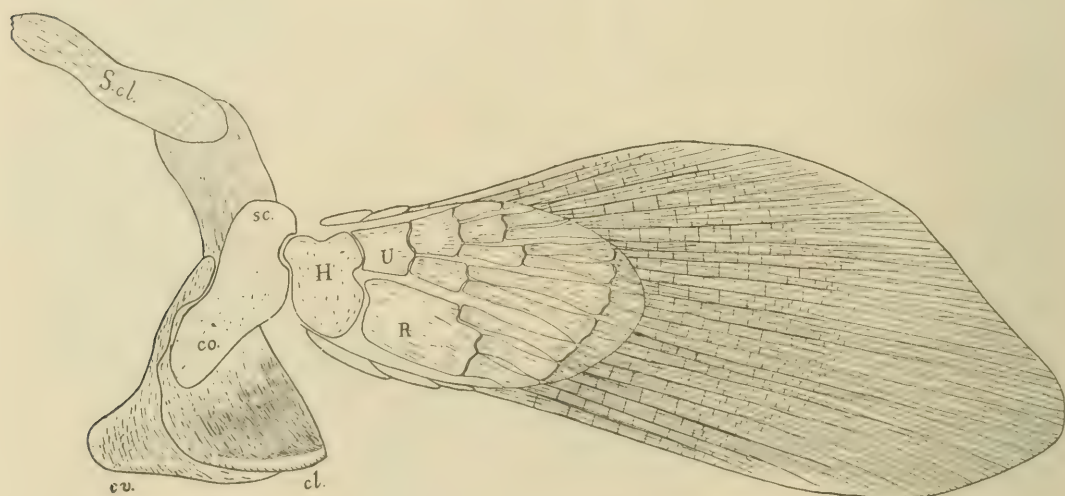


FIG. 9.—Right pectoral limb of *Sauripterus taylori*—Restoration, medial aspect

An Upper Devonian rhizodont rhipidistian. The known parts are shown in Plate I; the remaining parts are restored from the allied genera *Tristichopterus* and *Eusthenopteron*, except the coracoscapula, which is known only from the articular portion and is conjecturally restored from analogy with *Ceratodus*.

The mesopterygial series, homologous with the central axis of the "archipterygium" of dipnoans, Holoptychiidae, etc., is represented by the humerus, ulna and distally succeeding elements; the preaxial radials are barely represented; the postaxial elements form the major part of the fin skeleton and converge toward the mesopterygial axis.

we have actually seen, without attempting to restore any missing parts. Areas where the bone has been flaked off, leaving a clear impression in the matrix, are stippled; cracks and other adventitious features are omitted. Unfortunately most of the scapulocoracoid, the clavicle ("infraclavicle") and the greater part of the fin-rays are missing, and hence we do not know their precise shape, but have nevertheless attempted a provisional restoration (Fig. 9) restoring the missing parts chiefly from the allied genera *Tristichopterus* and *Megalichthys*. The fleshy, scaly lobe of the fin is indicated by the heavy, curved line. It is not known whether the ascending bar of the clavicle was present as in *Rhizodus* or absent as in *Strepsodus* (A. S. Woodward, 1891). We also give for com-

parison with *Sauripterus* a figure of an American Museum specimen referred to *Osteolepis microlepidotus*, showing the head, shoulder-girdle and pectoral fin (Fig. 10).

Further consideration compelled me (1912, p. 220) to give up the idea that the ascending blade of the shoulder-girdle in Rhipidistia represents the scapulocoracoid of Tetrapoda, partly because the type of *Sauripterus taylori* retains a portion of an element that lies between the ascending blade and the "humerus" or single proximal piece. The rest of this element probably covered a part of the medial surface of the dermal ascending blade and may have been present in the counterpart of the



FIG. 10.—Head and pectoral limb of *Osteolepis microlepidotus*

Crushed specimen in the American Museum (No. 7715). Slightly less than natural size. The massive cleithrum is partly overlapped by the operculum and suboperculum. The pectoral fin shows the large scales or plates covering the "humerus," the elongate plate covering the postaxial element, or "radius," the scales on the fleshy part of the fin and the dermal rays.

type, which was not obtained. In *Ceratodus* (Fig. 5) a corresponding piece is apparently homologous with the scapulocoracoid element of tetrapods, which is of course a cartilage bone. I therefore return to Gegenbaur's view (1895), which is also that of Dr. Broom, that the ascending blade in *Sauripterus* represents the cleithrum of primitive Stegocephali, although in them it is much reduced and the scapulocoracoid correspondingly enlarged. Accordingly the homologies of the elements of the pectoral limb in Rhipidistia and primitive Tetrapoda (Fig. 11) appear to be as follows:

RHIPIDISTIA

Interclavicular corium
Clavicle ("infraclavicle")
Supracleithrum ("supraclavicle")

Post-temporal
Coracoscapula

TETRAPODA

Interclavicle
Clavicle
? Fused with top of cleithrum (cf. *Sclerocephalus*)
Lost
Coracoscapula

Fleshy lobe of fin	Arm and hand
Mesopterygium (single basal piece)	Humerus
Mesopterygial axis	Humerus, ulna, ulnare, digit V (?)
Preaxial parameres (radials) reduced or absent	Lost
Postaxial parameres	Radius, carpus, digits I-IV (?)
Dermal rays	Lost

The pectoral limb of *Sauripterus* differs from the tetrapod type in the following characters: (1) In *Sauripterus*, as in other Rhipidistia, the chief ascending blade of the shoulder-girdle is formed by the cleithrum, the scapulocoracoid is small and the articular region is protuberant; whereas even in the most ancient known Tetrapoda the cleithrum is of relatively small size, the chief ascending blade is formed by the scapulocoracoid, and the articular region is sunk below the plane of the surrounding parts. (2) The dermal rays (lepidotrichia) are well developed (lost in Tetrapoda; *cf.*, modern Dipnoi). (3) The limb is articulated more on the postero-interior border of the ascending blade than on its outer face, and is directed backward rather than outward and downward. (4) The supposed radius, ulna, carpals and digits differ widely in form from these elements in the Amphibia, so that their supposed homologies are only recognizable after close study. (5) The successive segments of the limb apparently were not sharply inclined to each other, as at the elbow and wrist of Tetrapoda, but were arranged radially more like the axonosts and baseosts of ordinary fins. (6) While the evidence is not positive, the distal rods seem to dichotomize and even the undivided radials exceed in number the digits of the tetrapod manus. (7) The fin as a whole conforms to the imperfect archipterygial type seen in *Megalichthys* and *Eusphenopteron*, rather than to the cheiropterygial type of tetrapods. While all these differences may be simply primitive characters, separating members of two distinct classes, nevertheless they raise the question whether the tetrapod resemblances in the pectoral fin of rhizodonts may not be fortuitous, and without phylogenetic significance: but in view of the differences in function of the *Sauripterus* paddle and a true cheiropterygium such underlying similarities as may exist can hardly be attributed to convergence, and when taken in connection with the resemblances in the skull above noted (pp. 332-337) they gain in importance.

Dr. Broom's view that the tetrapod cheiropterygium developed only from the anteroventral border of a pre-*Sauripterus* stage appears to me to lack adequate evidence. Nor do I consider the presence of dermal rays as unfavorable to the development of a cheiropterygium. The re-

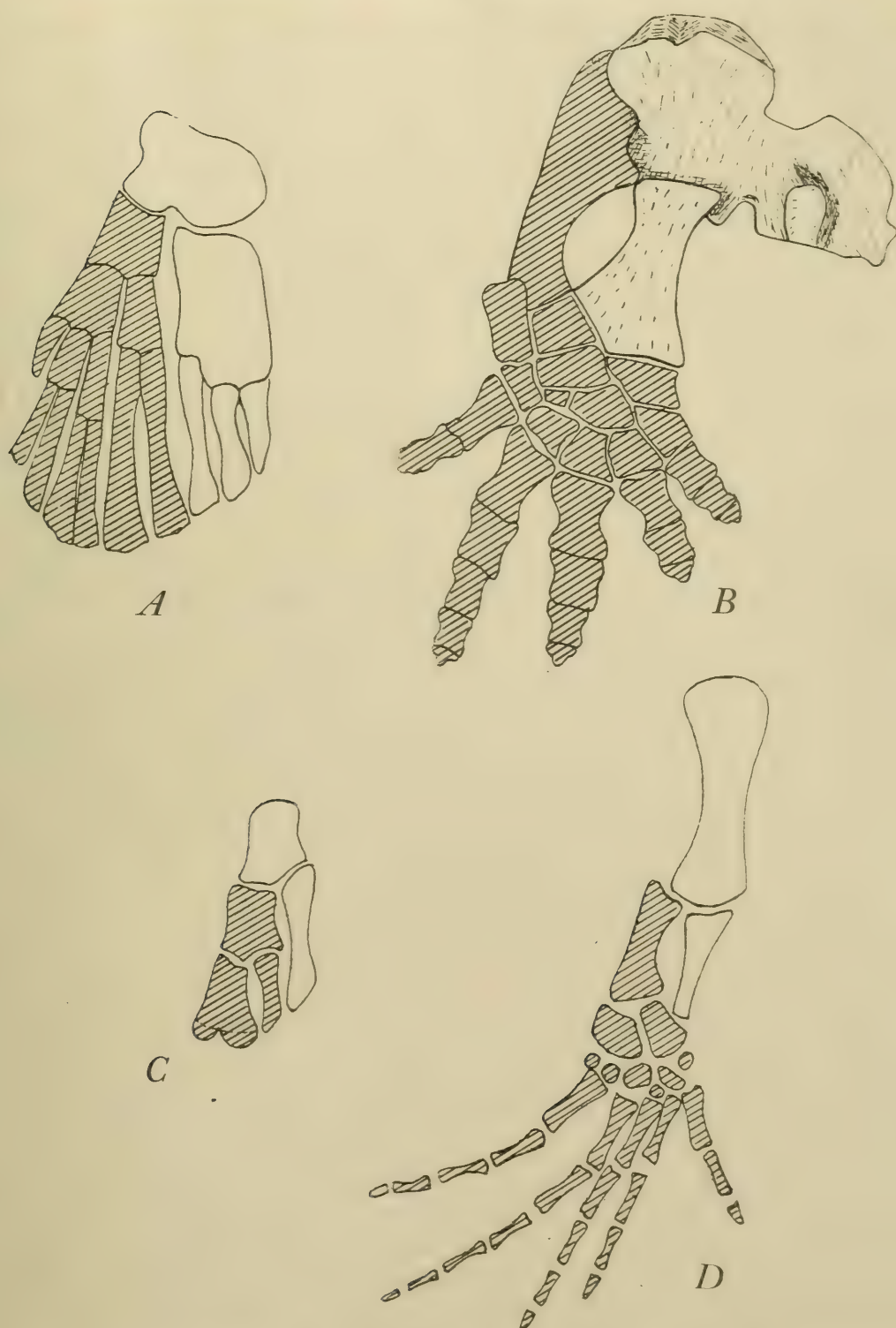


FIG. 11.—Comparison of the paired limbs of Palaeozoic rhizodonts and tetrapods

Left pectoral limbs of (A) *Sauripterus* and (B) *Eryops*. Medial or palmar surface. Left pelvic limbs of (C) *Eusthenopteron*, after Goodrich, and (D) *Eosaurus*, after Williston. Medial surface.

The elements that converge toward the mesopterygial axis (ulna, fibula) are hatched.

duction of the dermal rays has frequently occurred in the Actinopterygii (*e. g.*, *Muraena*, *Lepidosiren*) without impairing the locomotive power of the fish. When the pectoral fin was turned downward and forward the medial surface of the spreading lobate portion of the fin would seem to be fitted for the digital emargination of the borders and the modification of the radials to form the digits. Dr. H. H. Wilder (1909, p. 235) has also called attention to the fact that in the manus of *Necturus* the muscles for spreading and closing the digits are so highly developed as to suggest derivation from a primitive appendage which had the power of widely spreading and closing, as in the fins of fish. In *Sauripterus* (Fig. 10) and *Eusthenopteron* (Fig. 8) most of the radials converge toward the mesopterygial axis, which includes the supposed homologues of the humerus, ulnar, ulnare and digit V (?), and the same is true of the digits of the manus of Carboniferous Amphibia (Fig. 11) and Reptilia and of recent urodeles; in both classes the post-axial paramere, or radius, is sharply separated from the remainder of the cheiropterygium. I find that both Emery (1897, p. 208) and Jaekel (1909) have also noted this biramous character of the tetrapod cheiropterygium.

The muscles of the pectoral limbs of *Sauripterus* were probably separable into a deep proximal mass covering the scapulocoracoid and the humerus and a deep distal mass running from the humerus to the distal radials. Surface muscles perhaps extended from the radials back to the scapulocoracoid region. The joint corresponding to the elbow joint is clearly present in these rhizodonts and the "radius" and "ulna" are seen to be a part of the outer or distal segment of the limb.

The pelvic limb of *Eusthenopteron* (figured by Goodrich, 1909, p. 275), which is the best known one of the rhizodonts, has likewise a certain resemblance to the tetrapod type, as noted by Jaekel (1909), in so far as it possesses a single basal piece analogous to the femur and two main radials analogous to the tibia and fibula. The pelvic limb, like the pectoral, appears to represent an imperfectly attained mesorhachic type in which the preaxial elements have become more or less produced laterally and to some extent regrouped. The "femur" has two broad distal facets for the supposed fibula and tibia. The mesopterygial element, which may be called the "fibula," is a wide element bearing at its distal end two facets for the proximal "tarsals" which appear to be the fibulare and intermedium, or tibiale. The distal end of the supposed tibia, or preaxial paramere, lies beside the supposed intermedium; all the tarsals slant toward the fibular or mesopterygial axis. The joints corresponding to the knee and ankle joints are well defined (Fig. 11). All this constitutes a distinct resemblance to the pelvic limbs of Carboniferous Tetra-

poda (*cf.* Jaekel, 1909, Figs. 2-18), the great difference being that in the tetrapod the tarsals have become relatively shortened and wider while the metatarsals and digits, the tibia and femur have lengthened.

The stout pelvic bones appear to represent the ischio-pubis. No known representative of the ilium is present in the rhizodonts; but even in such relatively advanced tetrapods as *Eryops*, although the ilium is very large, it has not yet gained a secure contact with the backbone, and we must either suppose that the dorsal growth of the pelvic cartilage followed very rapidly upon the change in function from fins into supporting limbs; or possibly that the anterior process of the "ischio-pubis" of *Eusthenopteron* became rotated upward and gave rise to the ilium, while the posterior expanded portion broadened out into the true ischiopubic mass.

STEGOCEPHALI

Between the oldest known Amphibia of the Coal Measures and all fishes, there remain profound structural differences which are as yet unbridged by palæontological discovery. Even the branchiosaurs and their still more degenerate modern successors the urodeles have the dermal shoulder-girdle reduced and the epiphyses of their limb-bones cartilaginous, which may indicate that instead of being primarily aquatic animals, true links between fishes and terrestrial quadrupeds, they are secondarily aquatic (see also B. G. Smith, 1912, pp. 547-551). And yet in the larval state the branchiosaurs undoubtedly retained true piscine branchial arches, while the branchial skeleton of the Permocarboniferous "urodele" *Lysorophus*, as figured by Williston (1908), can leave no doubt of an ultimate piscine origin.

So wide are the differences between the various groups of Palæozoic Amphibia that one is led at first to inquire whether they may not have come off from different, but allied, groups of fishes, so that for example the Stereospondyli and the Temnospondyli might be related to the Osteolepidæ and Rhizodontidæ, while the Branchiosauria, Microsauria, Aistopoda and Urodela might conceivably run back to some form like *Tarrasius* (see pp. 357-358 above). Yet in spite of these wide differences among the Palæozoic Amphibia they all agree in having one fundamentally identical skull pattern and cheiropterygial limbs, so that present evidence suggests that the transformation of fishes into amphibians occurred but once.

This transformation involved first of all the abandonment of the tail as the principal propeller, the loss of its dermal rays, the abortion of the hypural bones and the assumption of the geophyrocercal form. Such a

transformation has occurred many times in the Actinopterygii and also in the Dipnoi. If the pro-Tetrapoda were Rhipidistia the transformation also involved the loss of the two dorsal and anal fins and of their expanded basal supports. The notochord in these pro-Tetrapoda must have been wholly persistent, for in the earliest known tetrapods the vertebrae are not only of widely varied type, but by no means complete. The pro-Tetrapoda undoubtedly had both the pectoral and pelvic fins strongly developed and of lobate or fleshy-based type. When they first emerged from the water, either in pursuit of littoral prey or during times of drought, they may have used the medial or palmar surface of the paddles for traction and propulsion, at the same time wriggling on their bellies. Some of those with small paddles soon adopted a snake-like habitus and lost the limbs (Aistopoda, Apoda). In those that developed the limbs (Fig. 14) the scapulocoracoid increased rapidly in size and became ossified, the cleithrum was reduced, the posttemporal and supracleithrum disappeared and the only connection between skull and shoulder-girdle was furnished by the "trapezius" muscle, which in modern urodeles extends from the "suprascapula" (? cleithrum) to the occiput (Fig. 14, F). Thus the shoulder-girdle acquired mobility, while, with the growth of the scapulocoracoid, its muscles acquired a larger base, and extended around from the medial to the external side. The extension of the coracoscapular muscles, ventrally, dorsally and externally, together with the differentiation of the pectoral muscles greatly increased the strength of the forearm and crowded the cleithrum to the front edge of the scapula. The differentiation of the pectoral muscles conditioned the formation of the rhomboid interclavicle which partly overlies them.

More difficult to comprehend are the muscular readjustments which must have ensued when the elbow and knee bends were being established, and the shifting of the articular surfaces of the humerus radius and ulna.

With regard to the muscles of the cheiropterygium itself, Professor H. H. Wilder (1909, pp. 230-231, 235) in the course of an illuminating discussion of the musculature of *Necturus* writes as follows:

"The muscles of the distal portion of the vertebrate cheiropterygium, that is, from elbow or knee on, aside from the modifications imposed upon them by the varying shapes of the limbs themselves, and the great difference in their use, are, in their essential features, quite similar in all living forms, and in their differences show the modifications of a primary type due to environment rather than the suggestions of an historic development of that type. The study is, therefore, one mainly of the adaptations of a given set of elements, rather than a phylogenetic history, which latter, as is the case also with the bones of the same region, must be sought in the gap separating fin and hand, that is, in the phylogenetic stages represented by lost forms of ganoids, stego-

cephali, and their allies. The salamander *Necturus*, probably the nearest approach to this series represented by living fauna, offers in its distal muscles some few suggestions of an earlier phylogenetic stage, and is thus of fundamental importance in the present inquiry. The well-nigh complete correspondence in the fore and hind limb as regards not only bones and muscles, but other parts as well, has been commented on above and offers strong support for the doctrine of serial homology, to be considered later. There are, also, as is the case with higher forms, some traces of a correspondence between the dorsal and ventral surfaces of a single paw, giving a suggestion of the derivation of the chiridial musculature from a fin-like precursor in which the jointed rays (digits) were supplied by similar muscular elements applied both dorsally and ventrally, as in present-day fishes. The following description is that of the anterior limb, but with the substitution of the terms *tibia* and *fibula* for *radius* and *ulna*, *tarsus* for *carpus*, and so on, it will be found almost equally applicable to the posterior one. In a few cases a muscle which is well developed in the anterior limb is small or wanting in the posterior, and thus the former is a little more typical.⁸

"Reviewing the conditions in this, probably the most primitive chiropterygium now left to us, several interesting points become manifest. The digits are moved in two ways, either flexed and extended or moved sideways, but while the system which provides for this latter form of motion is extremely well perfected, that for flexion and extension is not. For abduction and adduction there are typically five separate muscles for each digit, that is, two ventral, two dorsal and one intermetacarpal, while for flexion and extension, aside from the system supplied by an aponeurosis, and evidently a newly introduced feature, there are but three. *This extreme perfection of the sideways movement of the digits in the most primitive chiridium known, together with the weak and makeshift arrangements for bending and straightening the digits, strongly suggest the derivation of the chiridial type from one in which the digits (fin-rays?) required to be constantly opened and shut by lateral movements, precisely as in the case of the fins of most fishes.*

"During later phylogenetic history there is an evident tendency to increase the efficiency of the flexor-extensor system and diminish that of the abductors and adductors, except in the case of the two digits that form the ends of the series (I and V), and the most of these changes have already occurred among the higher urodeles."

As the skeletal remains of the limbs of Carboniferous Tetrapoda retain but little that is clearly suggestive of derivation from the paired appendages of fish, so too the footprints of these animals indicate that the

⁸ "In one point the free limb of *Necturus* diverges from what is generally believed to be the typical chiropterygium, and that is, it possesses but four digits in each extremity instead of the canonical five which is usually considered primitive. Since the nearest ally of this species, the cave form, *Proteus*, exhibits a still greater reduction of digits (anterior, 3; posterior, 2), it has been presumed that this is in both cases a secondary reduction. Certain facts, however, lead one to think that the first land vertebrates possessed a smaller number of digits than five, and if this be so, the condition in these two salamanders is primitive, and not a secondary reduction. According to the reduction theory digit I is assumed to be the one lost, and in accordance with this the four digits present are designated here, both in text and illustrations, as II-V." (Wilder, p. 231).

fleshy portions of the limbs were perhaps no more fish-like than in the modern *Necturus*.

These Carboniferous footprints vary widely in form, as do also the known skeletons of Carboniferous Tetrapoda. The number of toes in both manus and pes varies from three to five (G. F. Matthew, 1903, 1904), but in perhaps the majority of cases the manus has four digits and the pes five. Abel (1912, p. 68) indeed concludes that no stegocephalian had a five-fingered hand; but in a well known specimen of *Eryops megacephalus* (Amer. Mus., No. 4186) which was described by Cope (1880) digits I, III, IV, V are present in the fossil and the missing digit II is represented by a wide facet on carpal 2.

One of the oldest known footprints is a single impression from the Mauch Chunk Shale (Lower Carboniferous) of Pennsylvania to which the name *Thinopus antiquus* was given by Marsh (1896). The imprint consists of two stout, jointed toe-marks, which are nearly parallel to each other, but separated by a considerable interval extending back to the middle of the palm; from one of the toes a smaller offshoot near the tip indicates a small lateral toe. It may be a mere accidental resemblance that the pes of the modern *Proteus* is likewise bilobate, even in early stages of development (Wiedersheim, 1892, p. 199). A footprint named *Asperipes avipes* from the Carboniferous of Eastern Canada (G. F. Matthew, 1904, Pl. II, fig. 2a, 2b) represents a three-toed manus that may have been somewhat similar to that of *Thinopus antiquus*; but the pes of *Asperipes* has five digits.

Thus it is an open question whether the three- and four-toed feet of Carboniferous Tetrapoda represent reduction stages from the typical pendactyl cheiropterygium, or whether there has been an increase in the number of the digits from three to five. Favoring the former supposition is the following evidence: In modern Salamanders the number of digits is four in the manus and five to four in the pes; in the pes the process appears to have been reduction from five to four rather than the reverse: for, (a) in the development of the pes of the four-toed *Salamandrella kayslerlingii* there appears a vestigial fifth tarsal which later unites with tarsal 4 (Schmalhausen, 1910, figs. 6, 7), and (b) in the degenerate *Proteus* the number of digits is reduced to three in the manus and two in the pes.

In many of the Carboniferous footprints the fifth or outer digit of both manus and pes is sharply divergent, the fourth is the longest and the ends of digits IV, III, II, I are turned inward, while the foot as a whole points forward; all these characters suggest limb-structure fundamentally similar to that of *Eryops* or indeed of modern urodeles, especially the salamanders.

An important fact in connection with the origin of the tetrapod limbs is that in all known Carboniferous Amphibia and Reptilia as well as in recent urodeles all the digits, together with their carpals or tarsals, converge toward the ulna or fibula respectively, and that the whole carpus and tarsus are obliquely placed with reference to the ulna and fibula. This arrangement appears to be foreshadowed in the rhizodonts (Fig. 11) ; especially if we assume that only those radials that converge toward the mesopterygium were preserved, and that the postaxial radials gave rise to the vestigial prehallux and prepollex which are so widely distributed in the Tetrapoda (*cf.* Emery, 1897).

Although an ilium and a sacral attachment to the backbone are not known in fish, the readiness with which the backbone forms an attachment with the bases of the fins in different groups of fishes, either through the hypural bones, or, in the Rhipidistia, with the expanded bases of the dorsal and anal fins, indicates that with the enlargement of the hind limbs and pelvis the development of paired dorsal apophyses or ilia and their subsequent attachment to the sacral ribs would soon follow. Indeed the sacral ribs of *Eryops* and even of modern urodeles furnish an example of the imperfect connection between the pelvis and the backbone that existed in early tetrapods.

“PROCORACOID AND CORACOID” OR “CORACOID AND METACORACOID” ?

Notwithstanding all that has been written since Howes's paper (1887) in the effort to homologize the coracoidal elements throughout the Tetrapoda, investigators are still divided as to the application of these terms and as to the implied homologies. Professor Williston, in various publications, inclines to the view that the true mammalian coracoid is represented in the primitive reptiles by the anterior one of the two coracoidal elements; he accordingly calls it “coracoid,” while the posterior element he calls “metacoracoid”; other investigators, however (including Huene, Broom and Watson), continue to use the terms “procoracoid” and “coracoid.”

With the hope of coming to some decision in the matter I have compared the shoulder-girdle of representative Tetrapoda of all classes and Professor L. A. Adams has prepared the series of figures (Figs. 12-15) here published. It seems to us that Broom's observations (1899) on the development of the shoulder-girdle of marsupials offer decisive evidence that the true coracoid is the main element that extends down to the sternum in embryonic marsupials (Fig. 12, A, B), but we regard the mesenchymatous anterior element called by Broom “procoracoid” as more probably homologous with the epicoracoid of the monotremes and lizards

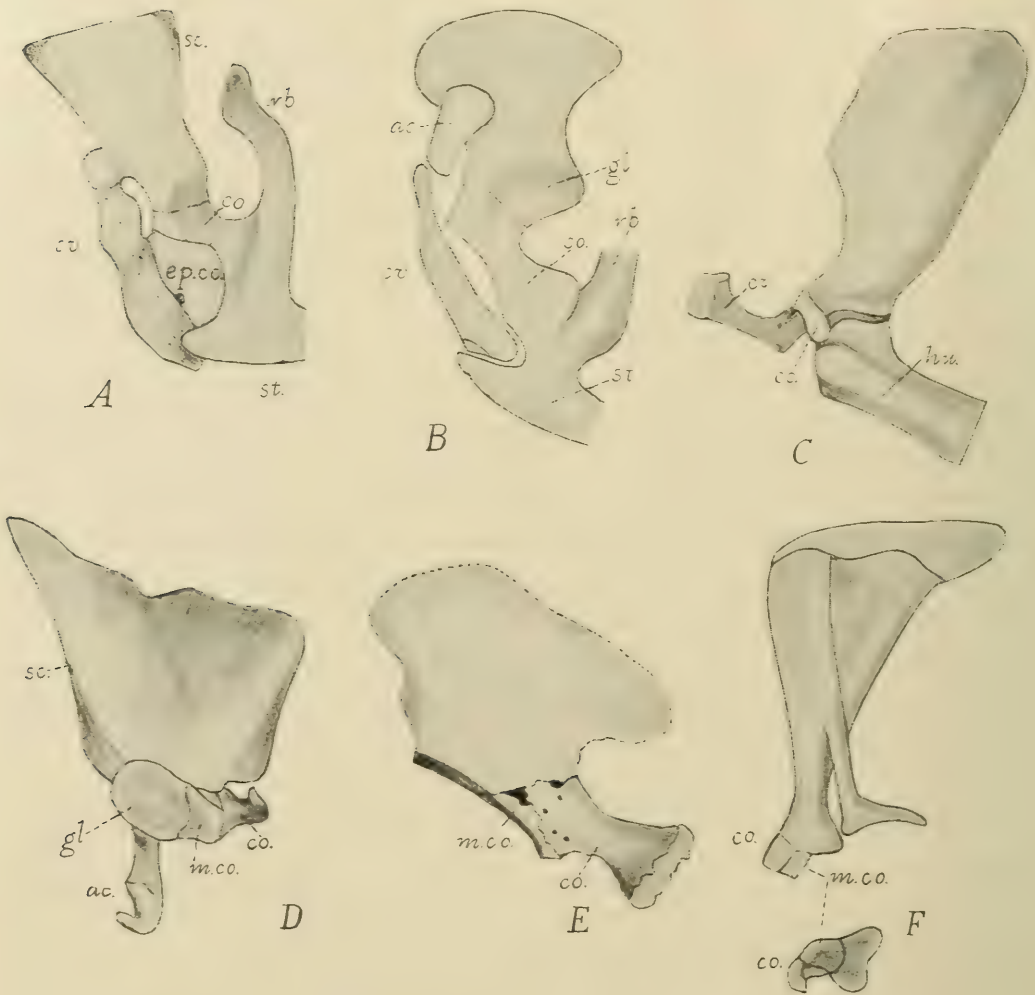


FIG. 12.—Homology of the coracoid in primitive mammals

A. Left shoulder-girdle (outer view) of an 8.5 mm. embryo of a diprotodont marsupial, *Trichosurus vulpecula*. After Broom. In this stage the true coracoid (cf. figs. B, C) is connected below with the sternum, as in adult monotremes. The epicoracoid ("procoracoid" of Broom) is mesenchymatous. It does not share in the glenoid and is therefore unlike the reptilian "procoracoid" (= coracoid), but does resemble the membranous epicoracoid.

B. Left shoulder-girdle (ventro-lateral view) of a 14.8 mm. *Trichosurus vulpecula* embryo. After Broom. The coracoid at this stage retains its connection with the sternum, which connection is lost in the adult; the epicoracoid has disappeared.

C. Right shoulder-girdle and proximal part of humerus (inner view) of adult diprotodont marsupial, *Phascolarctus cinereus*. The single coracoid shares in the glenoid and points downward and inward toward the sternum.

D. Left scapulocoracoid (ventro-medial view) of *Dasypus* sp., showing the metacoracoid (m.co.) as a separate element.

E. Lower part of left scapulo-coracoid of *Megatherium* (inner view), after Weber, showing suture between coracoid and metacoracoid.

F. Left scapulo-coracoid of *Lepus* (outer and distal views), after Howes, showing coracoid and metacoracoid both sharing in the glenoid articular surface.

(see below), and we do not favor Broom's view that the posterior, glenoid-sharing element (Fig. 12, D, E, F) in rodents, edentates and many other

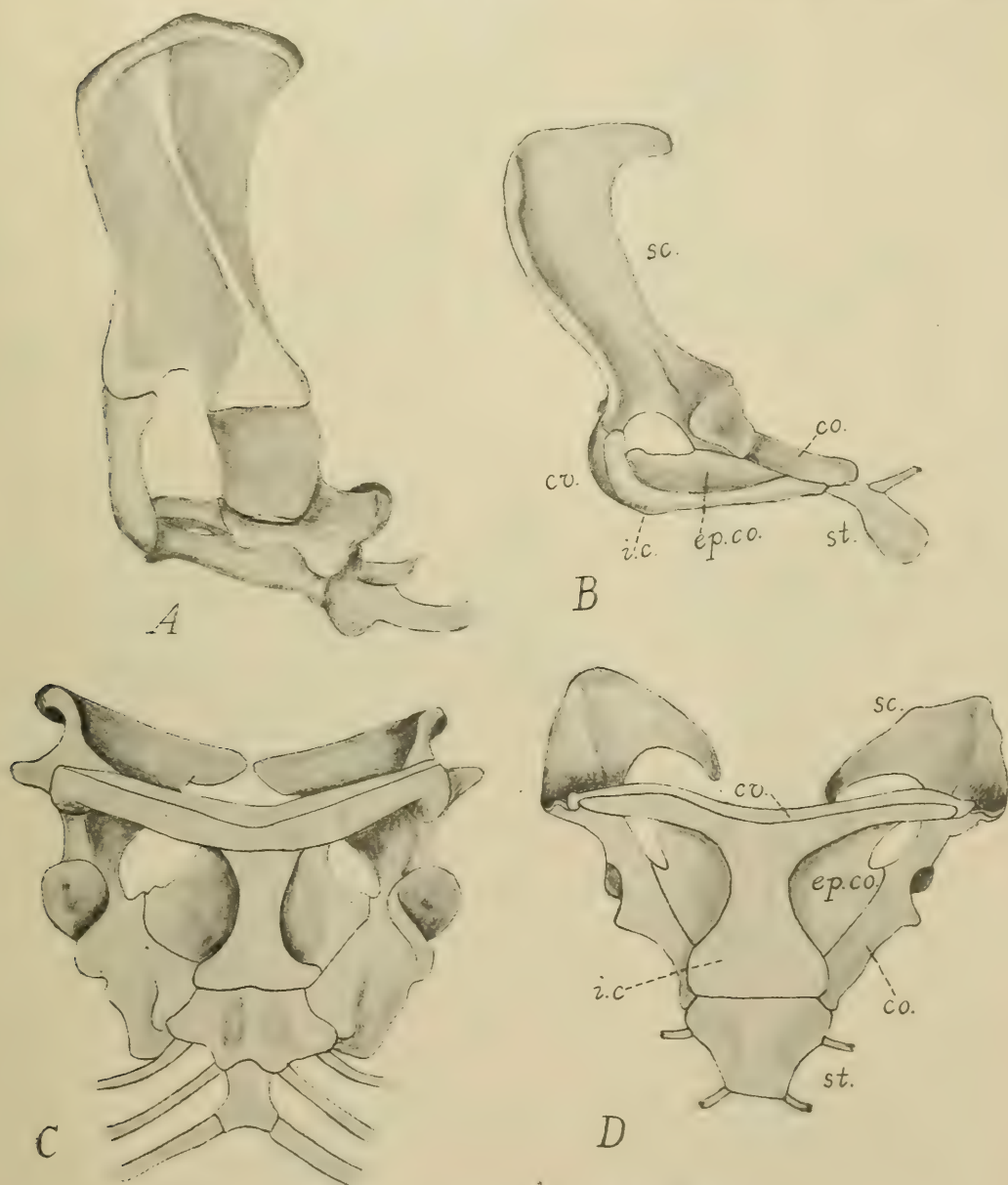


FIG. 13.—Homology of the coracoids in Monotremes

A, Shoulder-girdle of *Echidna aculeata*; B, *Ornithorhynchus anatinus*; left side, outer view; C, D, the same, ventral view.

The epicoracoid (*ep.co.*) agrees with that of lizards and *Sphenodon* in all its relations. The broad coracoid may either represent both the primitive reptilian elements (coracoid and metacoracoid) or the metacoracoid may have disappeared.

placental mammals is a neomorph, in the nature of a glenoid epiphysis. This so-called epiphysis agrees with the "metacoracoid" (Williston) of Permian reptiles (Fig. 14, E, F) in its relations with the true coracoid

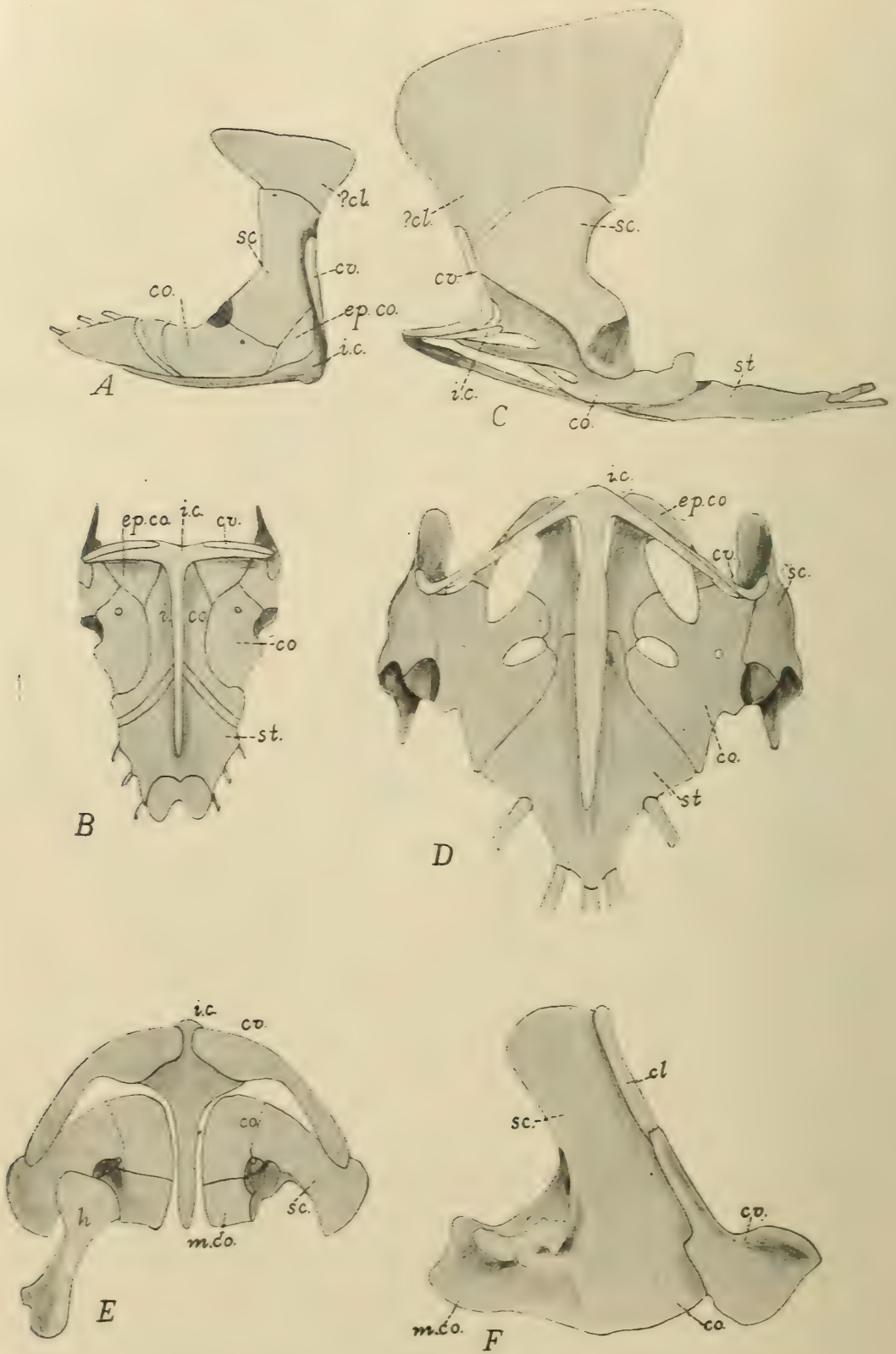


FIG. 14.—Homologies of the coracoids, etc., in reptiles

A, *Sphenodon*, right shoulder-girdle, outer view; B, ditto, ventral view. The coracoid is single. The metacoracoid may have disappeared. The epicoracoid (*ep.co.*) as in the lizard (C,D) is bounded by the scapula, coracoid, interclavicle and clavicle. Beneath the T-shaped interclavicle is the intercoracoid, or anterior sternal region.

C, *Varanus*, left shoulder-girdle, outer view; D, ditto, ventral view.

In *Sphenodon* and *Varanus* the so-called "suprascapula" (*?cl*) may possibly represent the cleithrum of primitive Tetrapoda (*cf.* Fig. 14 D). The "suprascapula," like the cleithrum, is connected below with the clavicle; to it is attached the trapezius muscle. The coracoid is single; anteriorly it is fenestrated for the pectoral muscles.

E, Shoulder-girdle of a Cotylosaur, *Labidosaurus*. Ventral view, after Williston. The coracoid and metacoid are distinct; the cleithrum is absent.

F, Shoulder-girdle of a Permocarboniferous reptile, *Edaphosaurus novomexicanus*, after Williston and Case. Right side. The expanded coracoid region, short scapula and large clavicle are perhaps inherited from primitive amphibians. The metacoracoid is present.

and with the glenoid; its wide distribution as a vestigial or reduced ossific center in various orders of mammals suggests that it is an ancient reptilian inheritance.

In reference to the shoulder-girdle of monotremes we would apply the name coracoid to the posterior element, which forms part of the glenoid (Fig. 13), since this part closely resembles the true coracoid of embryo marsupials. The anterior element (Fig. 13, *ep. co.*) may correspond with the epicoracoid (Fig. 14) of lizards and *Sphenodon*, as suggested by Wiedersheim (1909, p. 190), which never participates in the glenoid and always lies beneath the interclavicle and clavicle. Thus the true coracoid of monotremes may either have resulted from the loss of the suture between the coracoid and metacoracoid or the metacoracoid may have disappeared, while the epicoracoid has been developed, perhaps in adaptation to fossorial habits.

In the lizards, *Sphenodon* and other reptiles with a "single" coracoid (Fig. 14), this singleness may also have resulted either from the loss of the suture separating the coracoid from the metacoracoid, or from the disappearance of their coracoid. Their epicoracoid is also well developed and ossified.

In the lower Tetrapoda (Fig. 15), including various Permian orders, the coracoid and metacoracoid are often divided by suture, but the epicoracoid is not ossified.

In *Ceratodus* (Fig. 5), the sturgeons (Fig. 4) and the sharks, which have the best developed and largest coracoscapula cartilages among recent fishes, there is no sutural separation of parts and it seems likely that the segregation of ossific centres corresponding to the coracoid and metacoracoid is a later advance, perhaps correlated with the great expansion of the coracoscapular mass and the higher differentiation of the limb muscles in tetrapods.

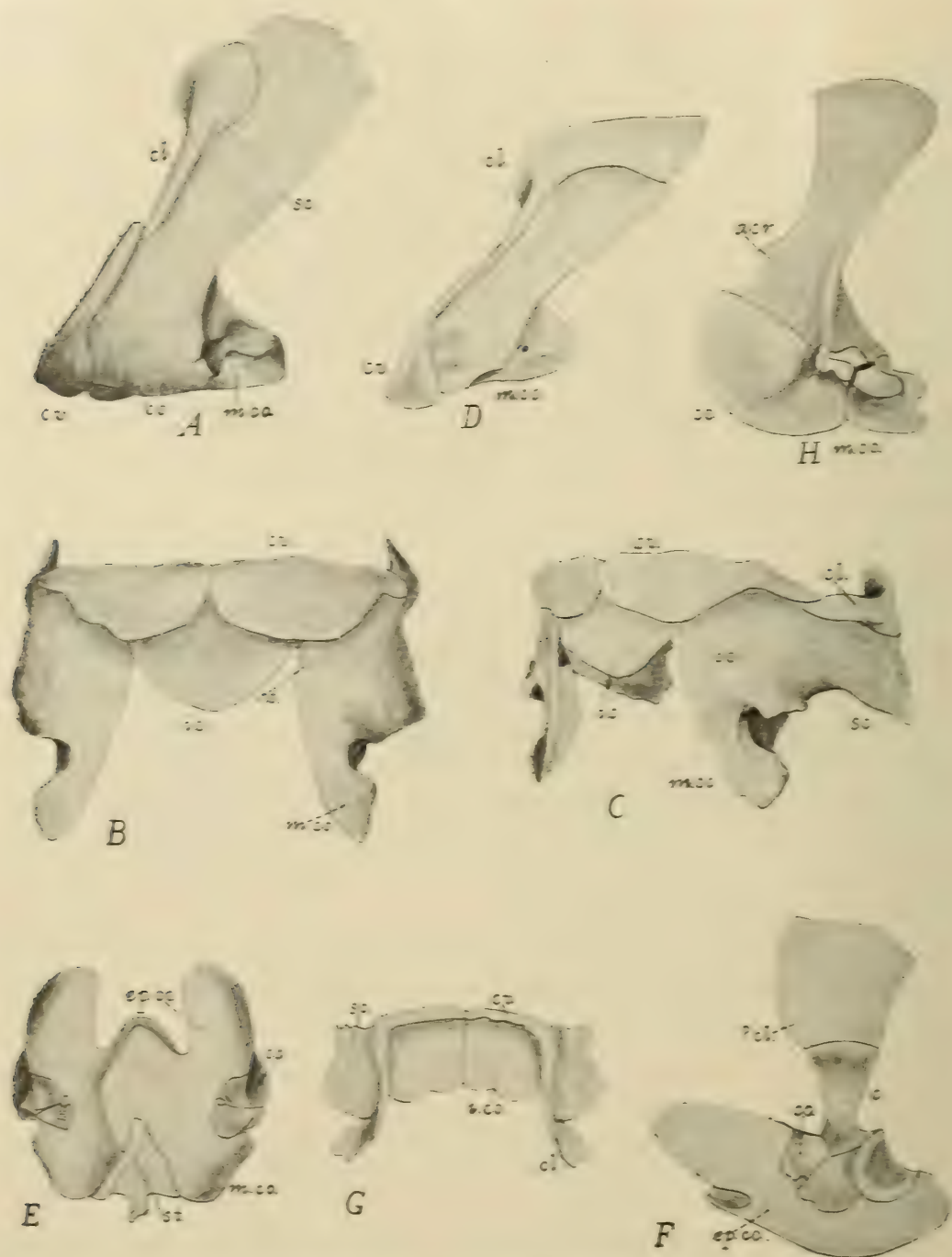


FIG. 15.—Homologies of the coracoids, etcetera, in Amphibia

A. Shoulder-girdle of a Permocarboniferous temnospondyl, *Eryops megacephalus*, outer view of left side; from specimens in the American Museum; B, the same, ventral view; C, the same, ventro-external view. (No suture between the coracoid and metacoracoid was found.)

All the elements of the primitive tetrapod shoulder-girdle are present. The median ventral space between the coracoids was probably filled by the intercoracoid mesenchymatous tissue.

Dermal elements: i.c., interclavicle; cr., clavicle; cl., cleithrum.

Cartilage bones: co., coracoid; m.co., metacoracoid; sc., scapula; gl., glenoid.

The expanded upper portion of the cleithrum may have served for the attachment of the trapezius muscle (*cf.* Fig. 14, F).

D, Shoulder-girdle of a Permocarboniferous temnospondyl *Cacops aspidophorus*. After Williston.

The cleithrum extends over the top of the scapula after the fashion of a suprascapula (*cf.* Fig. 14, F). The lower end of the cleithrum may represent the mammalian acromion (Gaudry, Broom).

E, Shoulder-girdle (ventral view) of a modern urodele, *Salamandra maculosa*, after W. K. Parker. Nearly adult, enlarged 4/1. The greatly enlarged intercoracoid cartilages, which overlap in the mid-line, furnish a broad base for the pectoral muscles. The anterior extension occupies the position of the epicoracoid. The interclavicle and clavicle are lost. *st*, sternum.

F, Shoulder-girdle (left side, outer view) of *Salamandra maculosa*, after W. K. Parker. Nearly adult, enlarged 5/1.

The coracoid, metacoid and scapula are still separated by sutures. The dermal elements are lost, except possibly the cleithrum (? *cl*), which may be represented by the so-called suprascapula; this gives attachment to the trapezius muscle.

G, Shoulder-girdle of a Permocarboniferous branchiosaur, *Brachiosaurus salamandroides*. After Fritsch. Viewed from above. $\times 6/1$. In the branchiosaurs, which are in many characters structurally ancestral to such modern urodeles as *Cryptobranchus*, the intercoracoids are much expanded, the scapula has a short truncate blade and the dermal elements (clavicle, interclavicle, cleithrum) are slender.

H, Scapulocoracoid of a Permocarboniferous reptile, *Dimetrodon*. After Williston. The expansion of the coracoid and the small size of the metacoracoid are reminiscent of the temnospondylous Amphibia. This scapulocoracoid is fundamentally similar to that of the Therocephalia and doubtless represents a pre-mammalian stage. *acr*, acromial process.

In short we conclude: (1) that in primitive reptiles the homologue of the true mammalian coracoid is that anterior element which: (*a*) lies below the acromial border of the scapula, (*b*) above the clavicle, (*c*) enters the glenoid articulation posteriorly and (*d*) extends ventrally toward the sternum; (2) that the posterior element or metacoracoid in many mammals persists in a reduced condition, arising from a separate center; (3) that in monotremes, lizards, *Sphenodon* and certain other reptiles the suture between the coracoid and metacoracoid may have disappeared or else the metacoracoid has disappeared (Williston); (4) that the epicoracoid is a thin membranous element lying between the coracoid and the interclavicle in lizards, *Sphenodon* and the monotremes, which was probably present also in many of the Permian Tetrapoda.

CONCLUSION

Although the foregoing discussion of the derivation of cheiropterygial limbs from piscine appendages is regrettably incomplete, it is at least based so far as possible upon the combined data of comparative anatomy and palæontology, and the evidence here summarized is, I hope, in line with the historical trend of development in these fields.

From the viewpoint which has been developed in the preceding pages, the origin of the Tetrapoda is regarded as a remote consequence of the

transformation of minute, acraniate, radially constructed coelenterates, moving by the lashing of cilia, and ingesting microscopic food particles, into pre-gnathostome animals with contractile myocoelomic pouches, which, becoming muscular, gave rise to the primary locomotive organs, or myomeres, as well as to the coelom.

Bilaterality ensuing, and pharangeal diverticula appearing, our animals entered the path of predatory adaptation; this led to the acquirement of accessory locomotive structures, including the local outgrowths called fins, and to the formation of a synthetic or gnathostome type of head, fitted for seizing and ingesting living prey.

The acquisition of a many-layered skin, proceeding with the further differentiation of the myocoelomic pouches, and of the derived mesenchyme, was followed by the development of an exoskeleton, and later of an endoskeleton, the mesenchyme carrying the bone cells either to the skin or to the mesenchymal connective tissue sheaths between the myomeres and around the dorsal axis.

Endoskeletal supports thus evolving the Osteichthyes appeared.

Of these the Dipnoi acquired elaborate tritoral teeth and other specialized conditions and thus removed themselves from the main ascending line, while in the other direction the Actinopterygii carried to a high perfection the scale-like dermal rays and other purely aquatic adaptations.

The Crossopterygii partly paralleled the Actinopterygii in the evolution of dermal rays but were distinguished by the outgrowth of fleshy lobate, fan-like paired fins, the prerequisites for the acquirement of hands and feet. The double-breathing pro-Tetrapoda reversed the direction of their evolution, sacrificed dermal rays, hypural bones, caudal and dorsal fins, scales, operculars, gulars and the elements connecting the shoulder-girdle with the skull, largely reduced the cleithrum and emerged from the water by virtue of the tractive and propulsive power of their stout paired fins.

As thus conceived the rise of the vertebrates and the origin of the Tetrapoda constitute a history of successive improvements in the locomotive apparatus.

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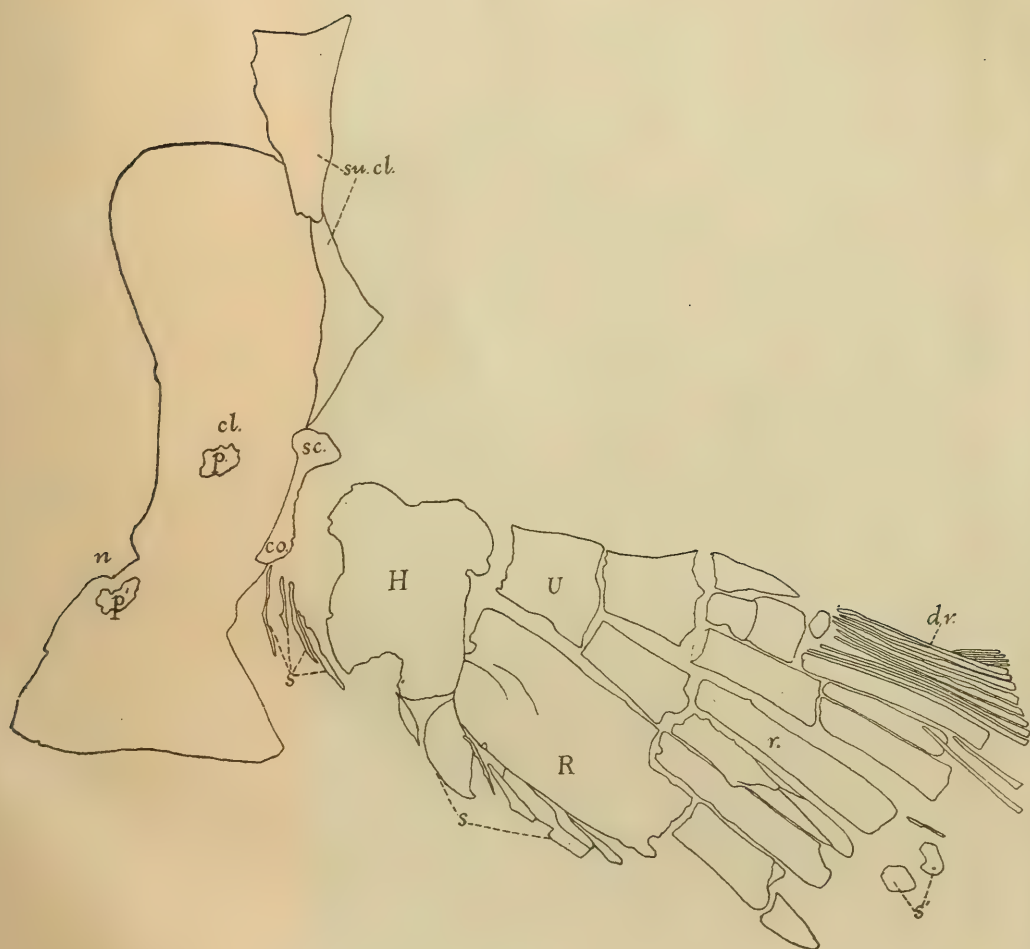
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RIGHT PECTORAL GIRDLE AND LIMB OF *Sauripterus taylori* HALL

Type, Amer. Mus. No. 3341. Internal, or medial, view. Two-thirds natural size.

cl, cleithrum; *su.cl*, ?supracleithrum; *co.sc*, remnant of coracoscapula, adhering to cleithrum and possibly represented also by the small patches *p*, *p'* (Broom); *n*, notch, possibly for ascending blade of clavicle; *S*, enlarged scales on metapterygial border; *S'*, scales on lobate portion of fin; *H*, single proximal basal piece, or humerus; *U*, mesopterygial axonost, or "ulna"; *R*, metapterygial axonost, or "radius"; *r*, radials; *dr*, dermal rays.



The figure is a study of a human form, possibly a woman, in a seated or crouching position. The drawing is very light and appears to be a preliminary study or a very light reproduction. It shows the outline of the head, torso, and limbs, with some internal lines suggesting clothing or anatomical details. The figure is facing towards the right side of the page.

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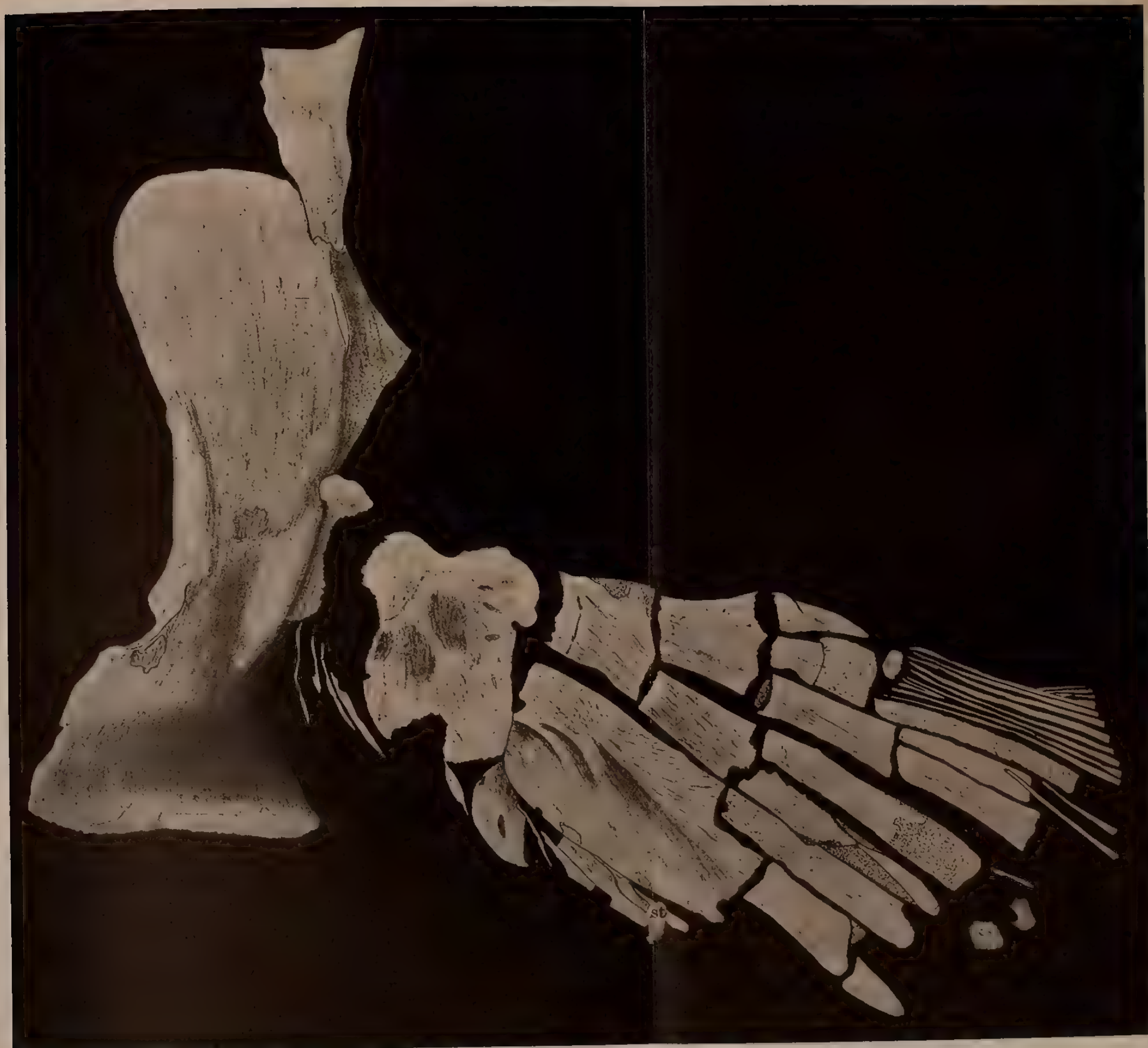
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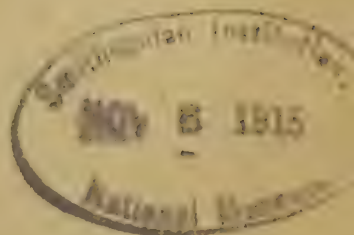
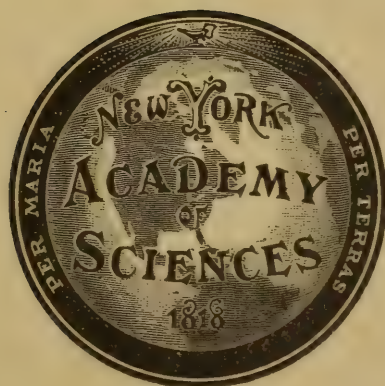
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BIOCHEMICAL STUDIES OF SELENIUM

BY

VICTOR E. LEVINE



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BIOCHEMICAL STUDIES OF SELENIUM¹

BY VICTOR E. LEVINE

(Presented in abstract before the Academy, 18 May, 1914)

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INTRODUCTION

There has been of late an ever increasing interest in the quest for information concerning the biologic action of the rare elements. Within the last few years attempts have been made to introduce radium, thorium, cerium, vanadium, tellurium and others into therapeutics; and it is but very recently that palladium has been suggested as a cure for obesity and selenium as a valuable agent in cancer therapy. Furthermore, selenium has become of increasing interest since it has been found (to the extent of 0.2 mg. per liter) in the mineral waters of La Roche-Posay, and since some of its compounds can serve as excellent reagents for the detection of certain alkaloids and also for the detection of micro-organisms.

The experiments undertaken extend the work, in this laboratory, which was done on selenium by Woodruff and Gies more than a decade ago.

¹ Manuscript received by the Editor 27 March, 1915.

The experiments relate to the reduction of selenium compounds by chemical substances of biologic significance, by micro-organisms, by plant substances and by animal tissues. Toxicological and pharmacological effects were also studied, as well as the effect on germination and growth of plants, the effect on enzyme activity and the effect on the precipitation of proteins. The compounds employed were selenium dioxid (selenious acid), sodium hydrogen selenite, normal sodium selenite, selenic acid, sodium selenate, potassium selenocyanate. For some of the compounds thanks are due to Professor Victor Lehner, of the University of Wisconsin.

SODIUM SELENITE AS A REAGENT FOR REDUCING SUBSTANCES

Sodium selenite in alkaline solution can be used as an indicator for reducing substances, especially for the carbohydrates containing a free carbonyl group. The following do not reduce sodium selenite (alkaline to litmus): acetone, formaldehyde, trioxymethylene, acetaldehyde, furool, benzaldehyde, cinnamic aldehyde, salicyl aldehyde, piperonal, methyl alcohol, ethyl alcohol, glycerol, erythrol, mannite, inosite, phenol, the cresols, thymol, α -naphthol, acetic acid, butyric acid, β -oxybutyric acid, palmitic acid, stearic acid, trichloroacetic acid, oxalic acid, tartaric acid, citric acid, oleic acid, malic acid, cinnamic acid, hippuric acid, glyocol, alanin, guanidin carbonate, leucin, urea, thio-urea, ammonium sulfo-cyanid, caffen, theobromin, uric acid, sodium urate, creatinin, lecithin, cholesterol, palmitin, stearin, olein, blood albumen, blood fibrin, edestin, egg albumen, gelatin, peptone, proteoses, ovalbumin, collagen, osseomucoid, elastin, saccharin, antipyrin, anthraquinone, sucrose, raffinose, cellulose, starch, dextrin, glycogen, inulin, esculin, amygdalin, and the following gums: arabic, tragacanth, guaiac, rosin, benzoin, kino, aloes, asafoetida, myrrh, gambir. Alcoholic solutions of benzoin, kino or aloes give a red-brown to cherry-red solution without the addition of sodium selenite. The following reduce sodium selenite: amidol, arabinose, rhamnose, xylose, dextrose, galactose, levulose, maltose, lactose, hydroquinone, phloroglucin, pyrogallol, hydroxylamin hydrochlorid, phenylhydrazin hydrochlorid, benzin hydrochlorid, hydrazin hydrate; arsenious, hydrobromic, hydriodic, phosphorous, hypophosphorous and sulfurous acids; ferrous sulfate, stannous chlorid, zinc and hydrochloric acid, hydrogen sulfid, acetylene, formic acid, gallic acid, lactic acid, tannic acid.

Acetone, acetaldehyde, formaldehyde, aceto acetic ester, β -oxybutyric acid, creatinin, lactic acid, formic acid and inulin reduce in acid but not in alkaline mixtures of sodium selenite. Methyl alcohol and ethyl alcohol reduce sodium selenite strongly acidified with sulfuric or with hydro-

chloric. Oxalic, citric, tartaric, malic and salicylic acids, benzaldehyde, cinnamic aldehyde, and salicyl aldehyde reduce neither in acid nor in alkaline mixtures.

The results show that monosaccharides readily reduce an alkaline solution of sodium selenite. The pentoses give readier and more profuse reduction than the hexoses and the reducing disaccharides. Of the pentoses, xylose yields most profuse reduction. Among the hexoses, levulose and galactose reduce more readily than dextrose, and galactose less readily than levulose. Among the disaccharides only those having a free carbonyl group reduce. Maltose and lactose show reduction, but sucrose does not. Raffinose, cellulose, starch, dextrin, glycogen, inulin also do not reduce.

In order to test the influence of acidity or alkalinity upon the reduction of sodium selenite, nineteen reagents were made up. One consisted of sodium selenite neutralized with sulfuric acid. Another consisted of sodium selenite, which reacts alkaline. To nine other selenite solutions were added sodium hydroxid, potassium hydroxid and Rochelle salts, sodium bicarbonate, sodium carbonate, and sodium citrate, sodium tetraborate, sodium silicate, disodium hydrogen phosphate. Eight reagents were acidified by the addition of one of the following: potassium bisulfate, sodium dihydrogen phosphate; hydrochloric, nitric, sulfuric, phosphoric, citric, or tartaric acid. When these reagents were heated none reduced, even on complete evaporation, except the one containing citric acid and the one containing tartaric acid. These two reagents also deteriorated after standing several months. Experiments with these reagents were carried on at 37.5° C. and at 100° C. Solutions (0.5 per cent) of arabinose, rhamnose, xylose, glucose, fructose, galactose, sucrose, maltose, lactose, glycogen, starch, dextrin, inulin, raffinose, mucic acid, lactic acid, formic acid, acetone and formaldehyde were used. Three cubic centimeters of the solution to be tested were mixed with two cubic centimeters of the selenite reagent and toluol added. The tubes were incubated at 37.5° C., and examined from time to time. Controls were run with the Fehling and the Fehling-Benedict reagents.

The reagents containing sodium hydroxid and potassium hydroxid (selenite and Fehling) were the first to show reduction at 37.5° C. The Fehling reagent reduced more quickly than the Fehling-Benedict. Glycogen, starch, dextrin, inulin and raffinose reduced acidified solutions of sodium selenite only at the end of four days. Alkaline solutions were not affected. Formic acid, lactic acid, formaldehyde reduced in acid solutions only. Acetone profusely reduced acid solutions, and very faintly reduced alkaline solutions. The reagent acid with nitric showed no reduction,

except in the case of acetone. Neutralized sodium selenite proves to be a very ineffective indicator for reduction. The presence of sodium tetraborate inhibits to a very striking extent the reduction of sodium selenite.

The reagent containing 2% sodium selenite, 10% sodium citrate and 10% sodium carbonate has been tested with reducing sugars. Reduction with this reagent takes place, at 100° C., in one minute or even less. At first a deep chlorine-yellow color is developed. After standing a minute or two this color gives way to a light wine-red tint, then to a dense brick-red precipitate, which fills the volume of the tube. A 0.02% solution of glucose yields fair reduction, and in a 0.01% solution the reaction is still evident, but faint. Solutions to be tested must be alkaline, and must not contain potassium cyanid or oxidizing agents (free halogen, hydrogen peroxid, potassium permanganate, potassium bichromate). Sugar-free urine gives a positive reaction when it is acidified with hydrochloric. This positive reaction is probably due to acetone substances and creatinin, which decidedly reduce acidified solutions of sodium selenite. Proteins, uric acid and creatinin do not interfere with the alkaline sodium selenite reagent.

Minute amounts of selenium in the form of selenite ion can be detected by a procedure similar to that of the Marsh test for arsenic. One milligram of selenium dioxid yields a characteristic dull red selenium mirror, soluble in oxidizing agents.

REDUCTION OF SELENIUM COMPOUNDS IN THE LIVING ORGANISM

PLANT SUBSTANCES

Plant substances (apple pulp and potato pulp) bring about the reduction of sodium selenite to brick-red selenium. An alkaline reaction favors the reduction process. Boiled material induces no reduction or very faint reduction.

YEAST

Yeast reduces selenious acid, selenic acid and sodium selenite. The red selenium deposits in the cell-body so that only the cells themselves are pigmented, while the liquid above remains colorless. The cells can be decolorized by washing with potassium cyanid.

UNBOILED MILK

Unboiled milk in contact with a few drops of sodium selenite (room temperature) will show reduction within one to three days; boiled milk will show no evidences of reduction. Unboiled milk protected with toluol does not reduce as readily as milk exposed to the air.

ANIMAL TISSUES

Animal tissues also reduce sodium selenite. Fresh liver, spleen, heart, lung, kidney, pancreas, small intestine, large intestine and stomach, incubated in the presence of toluol at 37.5° reduce a 0.5% solution of sodium selenite within twenty-four hours. The liver and spleen reduce very quickly and most profusely. Portions of striped muscle, testicles, thyroid, submaxillary gland and lingual glands give negative results. Toluol-preserved, unfiltered extracts, first kept at room temperature for twenty-four to thirty-six hours and then treated with sodium selenite showed reduction within twenty-four hours, only in the case of liver, pancreas and small intestine. This result indicates that the reducing power of the tissues disappears in the course of time. That the reduction is due to cell activity or enzyme activity is evident from the fact that tissues after being heated on a water-bath for about ten minutes fail to yield reduction. Fresh liver, however, heated or unheated, reduces sodium selenite. This reaction is due to the presence of chemically reducing substances such as carbohydrates. Tissues to which an excess of chloroform has been added show no reducing power. Chloroform itself does not inhibit the reduction of sodium selenite by pure sugar solutions. Filtered chloroform extracts also do not reduce, although the liver extract was found to reduce on the first or second day, and the spleen on the third or fourth day. The other extracts failed to show reduction, even after two weeks. Reduction is probably due to an insoluble enzyme closely connected with the living cell, that is, an endo-enzyme. Selenious acid and selenic acid are also reduced, while sodium selenate is not reduced.

SELENIUM COMPOUNDS INJECTED INTO THE ANIMAL SYSTEM

Selenium compounds, injected into the animal system, undergo reduction. Some of the selenium escapes from the organism in the form of a volatile organic selenid, some is precipitated, mostly extracellularly, in the tissues as dark red-brown granules. The liver and spleen contain by far the largest amount of deposited selenium. The microscopic examination of the histologically stained tissues of a dog that had received 2 mg. selenium dioxid per kilo, of body weight, revealed the presence of selenium in these two organs. With sodium selenite, selenium was found widely distributed in the liver, spleen, kidney, lung, pancreas, heart, stomach and intestine. These tissues showed marked reductions within the regions of hemorrhagic clots. Other tissues showed reduction only within such areas. A lethal dose of selenic acid brought about deposition of the granules in the spleen and liver. The lungs, which were found to be extremely congested, also showed reduction. Selenium pigmen-

tion with potassium selenate was slight in comparison with that produced with sodium selenite and but few granules were found scattered in the spleen, pancreas and liver. In the case of potassium selenocyanate, reduced selenium was found in the liver, spleen, lung, kidney, pancreas, heart, brain (only in hemorrhagic spots), muscle (only in similar spots) and stomach.

The reduction of selenium compounds seems to be a detoxicating process, since selenium itself is hardly poisonous. It seems evident that while sulfur compounds, such as sodium sulfite, are oxidized in the body to sulfate, the corresponding selenium compounds, such as sodium selenite, suffer reduction.

LIVING BACTERIA

Living bacteria bring about the reduction of selenious acid, selenic acid and sodium selenite. The precipitated selenium follows the path of bacterial growth. Granules of selenium can be observed under the microscope within the bacterial cell. The medium used should not contain reducing chemical substances, such as glucose or lactose. Sodium selenate is not reduced. Due to decomposition induced by acids, selenium may be also deposited from potassium selenocyanate. This happens to be the case with *B. coli*.

Reduction is proportional to the intensity of growth. Selenious acid, selenic acid and, less markedly, sodium selenite do not favor growth. The amount of retardation depends upon the nature of the organism. *Streptococcus pyogenes* was found to be more sensitive than *Bacillus coli*. The bacilli of symptomatic anthrax, edema, and tetanus are retarded very markedly in growth. Sodium selenate and potassium selenocyanate do not retard growth.

Selenium dioxid or sodium selenite cannot be used as a differential test between aerobic and anaerobic organisms, since the latter class also bring about reduction. There seems to be no specific relationship between selenium reduction and hydrogen sulfid production as Gloger maintained, since micro-organisms, such as *B. acidi lactici*, *B. diphtheria*, *B. pseudo-diphtheria*, *B. tuberculosis* that produce no hydrogen sulfid or only traces, were capable of reducing selenium dioxid or sodium selenite.

For practical purposes selenium dioxid or sodium selenite in concentrations of 1:50,000 or 1:25,000 can be used to demonstrate bacterial reduction. This phenomenon can also serve as a qualitative test for the selenite ion, even if the selenious acid or the sodium selenite is present in culture media in such small concentrations as 1:100,000.

EFFECT OF SELENIUM COMPOUNDS UPON CATALASE AND OTHER
ENZYMES

CATALASE

The compounds of selenium employed in enzyme investigations were selenium dioxid (selenious acid), selenic acid, sodium selenite, sodium selenate and potassium selenocyanate. The effect upon catalase was determined as follows: Healthy, normal dogs were bled to death from the femoral artery, using cocaine as a local anesthetic. Weighed amounts of defibrinated blood and tissues were ground with sand and mortar, treated with 40 c. c. distilled water and 10 c. c. chloroform and permitted to extract twenty-four hours. These served as controls. Equal amounts of blood and tissue were treated in the same manner, except that the distilled water was substituted by a 1/20% solution of selenium acid or a 1/10% solution of a selenium salt. After the extraction period a definite volume of the filtrate was treated with 5 c. c. Oakland dioxygen and the catalytic powers of the filtrate as measured by the volume of oxygen evolved, determined for every thirty seconds. The liver, kidney and blood showed the greatest catalytic activity.

The compounds of selenium investigated had a marked inhibitory effect on catalytic activity. Thus ten grams defibrinated blood evolved 52 c. c. oxygen in 7 minutes, another sample of the same blood treated with 0.05% selenium dioxid evolved 49.8 c. c. in 21 minutes, a third sample of the blood treated with 0.05% selenic acid evolved 52.6 c. c. in 14 minutes.

Blood from another dog yielded 44.8 c. c. in 9 minutes, another sample of the same blood treated with 0.1% potassium selenocyanate evolved 37.7 c. c. in 22 minutes. Control liver extract yielded 52.7 c. c. in 2 minutes; selenited liver extract yielded 50.2 c. c. in 8.5 minutes; selenated liver extract, 49 c. c. in 4 minutes. Another control liver gave 45.5 c. c. in 5.5 minutes, while another sample of the liver treated with potassium selenocyanate yielded 41.7 c. c. in 13.5 minutes. Generally speaking, the blood, liver, kidney, lung and spleen showed marked decrease in catalytic activity, the decrease sometimes being as much as 60% or over. Compared on the basis of equipercantages, it was found that selenium dioxid was more harmful than selenic acid, and that sodium selenite produced greater inhibition than sodium selenate. It is interesting to note, however, that colloidal selenium (prepared by the reduction of sodium selenite by glucose) brought about a slight acceleration in catalase activity.

Tissues of dogs killed with selenious acid, with selenic acid or with potassium selenocyanate showed no reduction in catalase values. This fact points to the decomposition of the selenium compounds injected, with the formation of substances that had no inhibiting effect on catalase action.

SALIVARY AMYLASE

The influence on salivary amylase was determined by Wohlgemuth's method. Small amounts of sodium selenite (neutralized) and sodium selenate (0.05% to 0.1%) had a slight effect on ptyalin. In the presence of 0.05% sodium selenite and, more markedly, in the presence of 0.05% sodium selenate the activity of the amylase seemed slightly increased.

The presence of potassium selenocyanate in the saliva or in the urine interferes with the Fehling-Benedict reduction test.

PEPSIN

The results obtained with pepsin showed that selenious or selenic acid could replace the hydrochloric acid of the gastric juice. Selenious acid was slightly inhibitive, while selenic acid resembled sulfuric acid in the marked inhibition which it shows towards proteolysis. Sodium selenite (neutralized) and sodium selenate (0.01% to 0.2%) had little or no effect on peptic activity. Higher concentrations produced inhibition, this being more marked with sodium selenite than with sodium selenate. Potassium selenocyanate, even in minute amounts, inhibits digestion, this probably being due, in part, to the mechanical interference of the brick-red precipitated selenium, which completely covered the fibrin, or possibly to the presence of the compound that results from the acid decomposition of potassium selenocyanate.

TRYPSIN

Slight amounts of sodium selenate and potassium selenocyanate had no effect on tryptic activity. Neutralized sodium selenite inhibited even in small quantities.

RENNIN

Sodium selenate and potassium selenocyanate (0.05%-0.5%) had no influence on rennin. Coagulation was retarded by concentrations of neutralized sodium selenite above 2%. Sodium selenite and sodium selenate had but a slight effect on the souring of milk. Potassium selenocyanate showed an inhibitory effect, the amount of inhibition being directly proportional to the concentration of the salt.

PANCREATIC LIPASE

Sodium selenate and potassium selenocyanate had no effect on pancreatic lipase. Sodium selenite had a slight inhibitory effect, which was proportional to the concentration. Experiments carried on with selenium dioxid and with selenic acid showed a marked increase in acid content. The high results can be attributed to the hydrolytic stimulation of these selenium acids.

ALCOHOLIC FERMENTATION

Selenium dioxid in concentrations of 0.5% had marked inhibitory action on alcoholic fermentation. In a 2.5% solution fermentation occurred, but was suppressed entirely in a 3% solution. Sodium selenite (alkaline) inhibited the evolution of carbon dioxid. Selenic acid, even in a concentration of 0.04% exercised an inhibitory influence over zymase. Very little carbon dioxid was evolved with a 0.2% solution, while solutions containing 0.5% or over gave no evidence of carbon dioxid formation. Sodium selenate accelerated alcoholic fermentation. The effect produced by potassium selenocyanate seemed to be variable, although, in general, the inhibition produced by concentrations lower than 2.5% was slight.

TOXIC EFFECTS OF SELENIUM COMPOUNDS

Selenium compounds are toxic to both plants and animals. Even concentrations of 0.01% inhibit germination and growth. Sodium selenate is the least toxic of the compounds investigated. Beginning with the most poisonous the sequence of toxicity for animals is hydrogen selenid, selenious acid, selenic acid, sodium hydrogen selenite, sodium selenite, potassium selenocyanate, sodium selenate and free selenium. Potassium selenocyanate is more toxic than the corresponding potassium sulfo-cyanate.

In very minute doses selenium compounds have no effect on blood pressure. In comparatively larger doses a marked fall in blood pressure is observed in the case of selenious acid, selenic acid, normal sodium selenite, sodium hydrogen selenite and sodium selenate, although with potassium selenocyanate a considerable rise in blood pressure is induced.

Selenium compounds, even in small doses, have a marked effect on respiration. Breathing becomes prolonged, deep and labored, and as the dose is increased respiratory paralysis sets in even before the heart stops. Pulmonary edema, accompanied by exudation of large volumes of yellowish fluid, precedes death in the case of selenious acid, sodium hydrogen selenite, sodium selenite and selenic acid.

The characteristic odor of a volatile selenium compound (methyl selenid ?) is scented in the animal's breath almost immediately after intravenous injection and about ten or fifteen minutes after subcutaneous injection. In one case, where the dose was five times the lethal dose, the odor was not evident. Another characteristic effect of selenium poisoning is the withdrawal of free hydrochloric acid from the stomach.

To account for the toxicity of the selenates we put forth the proposition that the selenates are reduced to selenite and finally to free selenium. To explain the toxic properties of sodium arsenate, Binz and Schulz claim that the arsenate is reduced in the animal body to the more toxic arsenite.

The selenium compounds investigated do not precipitate proteins from their solutions.

The author gratefully acknowledges his indebtedness to Professor William J. Gies for kind assistance, valuable suggestions and helpful criticism.

*Biochemical Laboratory of Columbia University,
College of Physicians and Surgeons.*

PLATE V

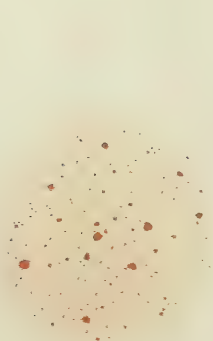
ILLUSTRATIONS OF BIOLOGICAL REDUCTIONS OF SELENIUM COMPOUNDS

FIG. 1.—*B. coli* grown on a sodium selenite culture medium. The colonies appear as red spots.

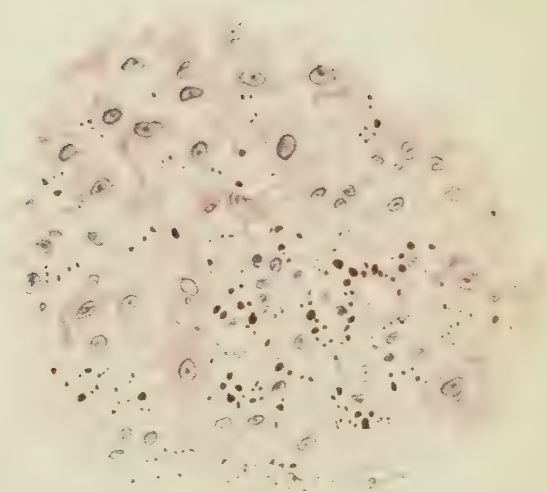
FIG. 2.—Another culture of *B. coli* grown on a slant.

FIG. 3.—Section of the liver of a dog that had been subcutaneously treated with 2 mg. selenium dioxid per kilo of body weight. The chocolate red granules represent deposited selenium.

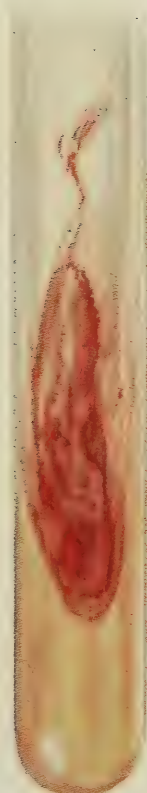
FIG. 4.—Stab culture of streptococcus pyogenes.



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OF THE
NEW YORK ACADEMY OF SCIENCES
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ANNALS OF THE NEW YORK ACADEMY OF SCIENCES

Vol. XXVI, pp. 395-486

Editor, EDMUND OTIS HOVEY

RECORDS OF MEETINGS

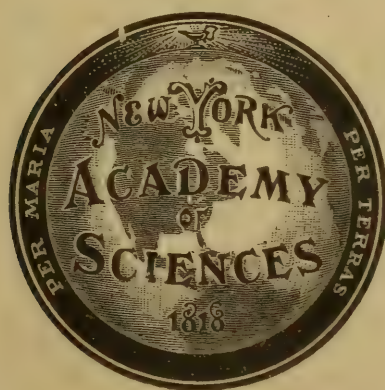
AND

MEMBERSHIP IN 1915

OF THE

NEW YORK ACADEMY OF SCIENCES

WITH INDEX TO VOLUME XXVI



NEW YORK
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12 MAY, 1916

THE NEW YORK ACADEMY OF SCIENCES

(LYCEUM OF NATURAL HISTORY, 1817-1876)

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The sessions of the Academy are held on Monday evenings at 8:15 o'clock from October to May, inclusive, at the American Museum of Natural History, 77th Street and Central Park, West.

RECORDS OF MEETINGS
OF THE
NEW YORK ACADEMY OF SCIENCES

January to December, 1915

BY HENRY E. CRAMPTON, *Acting Recording Secretary*

BUSINESS MEETING

4 JANUARY, 1915

The Academy met at 8:23 P. M. at the American Museum of Natural History, President George F. Kunz presiding.

The minutes of the last business meeting were read and approved.

The following candidates for membership in the Academy, recommended by Council, were duly elected:

ACTIVE MEMBERSHIP

Mrs. M. Archer-Shee, Ashurst Lodge, Sunninghill, Berkshire, England,

George W. Brackenridge, San Antonio, Texas,

A. Clayburgh, 35 Thomas Street,

Raymond L. Ditmars, New York Zoölogical Park,

Mrs. E. C. T. Miller, 3738 Euclid Ave., Cleveland, Ohio,

Barrington Moore, 40 East 83rd Street,

Elam Ward Olney, Convent, New Jersey,

Max W. Stöhr, 136 Pennington Avenue, Passaic, N. J.,

Stephen Dows Thaw, Morewood Place, Pittsburgh, Pa.,

Walter Harvey Weed, 29 Broadway,

Arthur L. Wessell, 457 West 45th Street.

The Recording Secretary reported the following deaths:

Mrs. P. Hackley Barhydt, Life Member of the Academy since 1907, died 6 March, 1914,

Miss Grace H. Dodge, Life Member of the Academy since 1907, died 27 December, 1914,

R. A. Canfield, Active Member of the Academy since 1905, died 11 December, 1914.

The Recording Secretary gave a brief summary of the report of progress made by Professor N. L. Britton, Chairman of the Porto Rico Committee, to His Excellency, Governor Arthur Yager of the Island of Porto Rico, showing that highly satisfactory work had been done during the year 1914 in reconnaissance and also in intensive work in geology and several branches of zoölogy as well as through the continuance of the botanical studies which have been carried on for several years by the New York Botanical Garden.

The Academy then adjourned.

EDMUND OTIS HOVEY,
Recording Secretary.

SECTION OF GEOLOGY AND MINERALOGY

4 JANUARY, 1915

Section met at 8:30 P. M., Vice-President Charles P. Berkey presiding. The following programme was offered:

- | | |
|-----------------------------|---|
| E. O. Hovey, | BIG SKOOKUM, MT. EDITH AND OTHER NEW AC-
CESSIONS TO THE METEORITE COLLECTION OF
THE AMERICAN MUSEUM. |
| James F. Kemp, | ORIGIN OF THE MAYORI IRON ORES OF CUBA. |
| Charles P. Berkey, | NOTES ON THE GEOLOGIC STRUCTURE OF PORTO
RICO. |
| Francis M. Van Tuyl, | SOME NEW POINTS ON THE ORIGIN OF DOLOMITE. |

The Section then adjourned.

A. B. PACINI,
Secretary.

SECTION OF BIOLOGY

11 JANUARY, 1915

Under the auspices of the Section of Biology, a general meeting of the Academy and its Affiliated Societies was held in the main lecture hall at the American Museum of Natural History at 8:15 P. M. President George F. Kunz presiding.

The following programme was then offered:

- J. C. Bose,** PLANT AUTOGRAPHS AND THEIR REVELATIONS.

SUMMARY OF PAPER

Professor **Bose**, of Presidency College, Calcutta, described and exhibited the apparatus devised by him for recording the reactions of plants to physical and chemical stimuli. The movements of the leaves and stems in response to stimuli are magnified by appropriate levers and electrical devices and are recorded as undulations upon a revolving cylinder. Records of the physiological reactions called sleep, fatigue, shock, recovery from shock and death were exhibited, as well as reactions to sunlight and other stimuli. Several of these processes were also demonstrated upon living plants.

After the lecture the speaker was the guest of honor at a reception given by the Academy, under the auspices of the Section of Biology.

WILLIAM K. GREGORY,
Secretary.

SECTION OF ANTHROPOLOGY AND PSYCHOLOGY

25 JANUARY, 1915

The Section met in conjunction with the American Ethnological Society, with Professor Franz Boas in the chair. The following programme was then offered:

John W. Chapman, THE MEDICINE-MEN OF ANVIK, ALASKA, AND VICINITY.

Rev. **Chapman**, after sketching his personal observations of shamanistic practices, described some of the fundamental native theories underlying them. One method of foretelling the future is to go to the moon, where the shaman meets his informants; another is to look into the bottom of wooden bowls and there see, as in a vision, what is to come to pass. The shamans enjoy a privileged position in native society. They pretend to ward off danger from individuals and exact high fees in return. The office is not hereditary, but seems based on the conviction becoming established that a certain man possesses extraordinary powers. The intellectual atmosphere in which such a belief may thrive is characterized by certain striking features. Honors and mortuary gifts are regularly paid to the deceased. It was formerly the custom to remove a corpse from the house through the smoke-hole rather than the usual exit. There were a number of feasts, some of a purely social potlatch type, others of a ceremonial character. One of these is noted for its pantomimic exhibitions. There is a belief in the survival of the soul after

death, special conditions being assigned to suicides and those who die by violence.

The lecture gave rise to many questions and comments by Drs. Boas, Goddard, Lowie, and Hatt. Dr. Hatt called attention to certain interesting similarities between Anvik and Lapp beliefs and customs.

ROBERT H. LOWIE,
Secretary.

BUSINESS MEETING

1 FEBRUARY, 1915

The Academy met at 5:30 P. M. at the American Museum of Natural History, President George F. Kunz presiding.

The minutes of the last meeting were read and approved.

The following candidates for membership in the Academy, recommended by Council, were duly elected:

ACTIVE MEMBERSHIP

Charles E. Slocum, 218 13th Street, Toledo, Ohio,

Henry J. Cochran, 389 Fifth Avenue,

Mrs. Rebecca McM. Colfelt, 925 Chestnut Street, Philadelphia, Pa.,

Marion Eppley, Princeton, N. J.,

Mrs. Catherine K. Blake, 138 East 37th Street,

Joseph A. Blake, Jr., 351 Yale Station, New Haven, Conn.,

James R. Steers, 1 West 70th Street.

The Recording Secretary reported the following deaths:

J. E. Parsons. Active Member of the Academy since 1896, died 16 January, 1915,

Mrs. M. A. P. Draper. Active Member of the Academy since 1898, died 8 December, 1914.

The Academy then adjourned.

EDMUND OTIS HOVEY,
Recording Secretary.

SECTION OF GEOLOGY AND MINERALOGY

1 FEBRUARY, 1915

Section met at 8:30 P. M., Vice-President Charles P. Berkey presiding. The following programme was offered:

Lawrence Martin, ALASKAN MOUNTAINS AND GLACIERS IN RELATION TO RAILWAY ROUTES.

The Section then adjourned.

A. B. PACINI,
Secretary.

SECTION OF BIOLOGY

8 FEBRUARY, 1915

Section met at 8:15 P. M., Vice-President Raymond C. Osburn presiding.

The following programme was then offered:

- G. S. Huntington,** SOME FURTHER CONSIDERATIONS UPON THE STRUCTURE OF THE VERTEBRATE LUNG.
H. von W. Schulte, SOME ONTOGENETIC VARIANTS OF THE HUMAN KIDNEY.
Alfred J. Brown, PHYLOGENETIC RELATIONS OF THE PELVIC GIRDLE IN MAMMALS.

SUMMARY OF PAPERS

Professor **Huntington**, continuing the report made during the previous year upon the collection of preparations of the lungs of vertebrates, in the Morphological Laboratory of the College of Physicians and Surgeons, illustrated many types of vertebrate lungs, especially among the reptiles and mammals, and said in abstract:

It is, of course, not only unnecessary, but quite inadmissible, to suppose that extant reptilian types, if sufficiently determined, would yield an unbroken and closely graded series of pulmonary types leading directly to the mammalian lung. All our evidence, comparative and ontogenetic, speaks to the contrary, and suggests that the pro-mammalian lung debouched from a reptilian type corresponding about to the simpler lacerilian lung of to-day, or at most advanced to the stage found in the more primitive modern paludal and littoral chelonians. Such an archeal lung presented the central pulmonary cavum still continuously lined by respiratory epithelium, before the introduction of the intrapulmonary bronchial system. The more complicated and highly organized lungs of the marine chelonians and of the Crocodilia are adaptations along the line of continued reptilian development, beyond the point of the mammalian derivation.

The hypothetical common pro-mammalian ground-plan of bronchial architecture, from which all extant types are derived by modifications, either in the direction of further expansion or reduction, does not exist in the commonly assumed form of a concrete, fixed morphological entity. The primitive pro-mammalian entodermal lung-tube, on the contrary, must, like its lacertilian prototype, have possessed the power of selective development of bronchial buds from any point of its epithelial surface.

The characters and type of such selections have been determined by environmental adaptations in the widest sense. They must have from the beginning represented the reaction of the milieu on pulmonary organization, and hence it is quite possible that we are dealing with a polyphyletic ancestry of the modern mammalian lung.

The extant ordinal types are the result of the transmission of selective patterns by inheritance to the modern descendants. All our evidence goes to show that the primitive lung form has, in certain groups, during the progress of evolutionary descent, undergone modifications—sometimes of wide import—in direct response to changes in the environmental adaptations of the organism as a whole. The possibility for the development of these secondary adaptive modifications lies in the continued morphogenetic plasticity of the lung tube—and in its potential capacity of developing additional or atypical points of epithelial activity.

The individual variants within a species—both secondary and cardinal—demonstrate the possession of this capacity conclusively. Mammalian ontogeny strongly confirms this view, which affords likewise the only key for the interpretation of the complicated ordinal divergence of bronchial types.

Professor **Schulte** illustrated a number of ontogenetic variants of the human kidney, such as deranged position, including inversion, of one kidney and its vessels, adhesion or partial fusion of both kidneys, complete union of the opposite kidneys into a single organ, varying degrees of atrophy of one kidney.

These abnormal conditions are made more intelligible by the ontogenetic history of the kidneys, the opposite kidneys arising in a very restricted space and migrating thence along divergent paths to their definitive positions. When the normal course of development is disturbed, the two closely appressed glands may adhere or more or less completely unite; in the subsequent displacement, or migration of the kidneys, one or the other is thus dragged out of its normal course and assumes irregular positions with reference to its fellow.

Doctor **Brown** illustrated certain abnormal conditions in the dorsal and lumbar regions of the vertebral column, characterized by asymmetri-

cal development of the free ribs, or of the vertebræ, or by the presence of supernumerary elements. Such abnormalities, he believed, may well be an expression of a general process of reduction in the number of the ribs and lumbar vertebræ, correlated with the upright pose in sitting and walking.

The speaker illustrated this hypothesis by means of a series of Primate skeletons, beginning with the tailed quadrupedal monkeys and culminating in the anthropoid apes and man.

The Section then adjourned.

WILLIAM K. GREGORY,
Secretary.

SECTION OF ASTRONOMY, PHYSICS AND CHEMISTRY

15 FEBRUARY, 1915

Section met at 8:15 P. M., Vice-President Charles Baskerville presiding.

The minutes of the last meeting of the Section were read and approved.

The following programme was then offered:

A. R. Rose, PHOSPHORUS COMPOUNDS IN RELATION TO ANIMAL AND PLANT LIFE.

I. S. Kleiner, ON THE GREATER RETENTION OF GLUCOSE INJECTED INTRAVENOUSLY INTO DEPANCREATIZED ANIMALS AND ITS RELATION TO PANCREATIC DIABETES.

SUMMARY OF PAPER

Dr. **Rose** said in abstract: The phosphorus compounds derived by the substitution of the H ions of phosphoric acid may be classified into two general groups, one, termed inorganic phosphorus, consisting of compounds in which the H ion has been replaced wholly or in part by metals; the other, organic phosphorus, in which one or more of the H ions have given way to organic radicals. In general, only inorganic phosphorus is available to plants, and hence all of these forms are not equally suitable to their nutrition. The soil from which the plant draws its food is rich in both organic and inorganic phosphorus. There are agencies present tending to change all forms into suitable nutrients. Within the plants the inorganic compounds are combined with more or less complicated organic substances, giving us the various forms of organic phosphorus with which we have to deal.

These constitute in large part the phosphorus nutrients of the animal

world, from which they pass almost wholly as inorganic phosphates and therefore suitable as plant food. The question of utility of the inorganic phosphorus in the animal economy is still a very much debated point. The organic phosphorus compounds synthesized by the plants may be divided into three general groups between which there are no sharp lines of demarcation: the phosphorus combined with protein; the phosphorus combined with fat-like substances; and the phosphorus otherwise combined, among which is a subdivision designated as phytosphosphates. This subdivision is to us at the present time the most interesting. The phytosphosphates occur in all plants and in most cases account for the major portion of the total phosphorus. They are obtained by extraction with acidulated water and then precipitating with alcohol or the heavy metals. The most prominent member of the group is thought to be a hexaphosphoric acid ester of inositol and is sold in the drug trade with absurd claims of therapeutic properties under the name of "Phytin." The constitution of this (or possibly these) substance (or substances) is not definitely established, but many of its properties have been agreed to by the several workers in this field. Because of its being a relatively large proportion of the phosphorus that enters the nutrition of man and beast it is considered as a very important substance. Its study in the growing plants justifies us in concluding that it plays a significant rôle in the growth of plants. It is also suspected that it enters specifically into the enzym actions and is a stepping stone in the synthesis of the more complex substances both free of and containing phosphorus.

The Section then adjourned.

E. E. SMITH,
Secretary.

SECTION OF ANTHROPOLOGY AND PSYCHOLOGY

22 FEBRUARY, 1915

Section met in conjunction with the New York Branch of the American Psychological Association at Columbia University, Professor R. S. Woodworth presiding.

The following programme was offered:

W. A. McCall, PRELIMINARY REPORT OF AN EXPERIMENT TO DETERMINE THE EFFECT OF AIR CONDITIONS UPON THE ACCURACY OF JUDGMENT OF INTELLECTUAL PRODUCTS.

Edith F. Mulhall, EXPERIMENTAL STUDIES IN RECALL AND RECOGNITION.

- M. A. Martin,** PRACTICE AND ITS TRANSFER EFFECTS IN CANCELLATION TESTS.
- R. S. Woodworth,** INFLUENCE OF RETENTION OF CONDITIONS FAVORING QUICKNESS OF LEARNING.
- J. J. B. Morgan,** THE ENERGY ERROR IN INTERFERENCE TESTS.

SUMMARY OF PAPERS

Mr. **McCall** said: It has been shown by Thorndike, Chapman and McCall that the effect of air conditions, ranging from 68° F., 50 per cent. relative humidity and 45 cubic feet of air per person per minute, up to 36° F., 80 per cent. relative humidity and the air unchanged and stagnant, was absolutely the same upon the product produced by and the rate of improvement of certain mental functions. This was true when the young men tested worked at maximal effort and were subjected to any one condition either one day of four hours or five consecutive days of four hours each.

The purpose of the experiment to be described was to ascertain whether this same lack of difference would be found when the conduct of the experiment and the nature of the tests were such as not to stimulate effort, but to encourage carelessness.

This experiment was conducted in the laboratory of the New York State Commission on Ventilation, where any desired ventilation condition could be very accurately maintained. The tests were made upon four male college students who occupied the experimental chamber for six consecutive weeks, five days to the week and seven hours to the day. Six air variables were employed, each condition lasting one week. The range of air conditions was the same as that noted above.

The psychological tests occupied the first three days in each week and consisted in having the subjects assign values to specimens of penmanship and English composition according to the Thorndike Scale for Handwriting and the Hillegas Scale for English Composition, respectively. In all 27,360 judgments were made. The exact value of each specimen of penmanship and composition has been determined and the average error of the subjects' judgments has been calculated for each of the air conditions.

The subjects also gave a numerical comfort statement. These comfort judgments have been averaged for each air condition. The results justify the following conclusions:

- 1). The hot humid conditions reduced the comfort of the subjects.
- 2). The comfort of the subject showed no demonstrable correlation with his accuracy of judgment.

3). The function tested was a highly variable one, but it varied irrespective of the time spent upon the test.

4). No one condition more than another affected detrimentally the accuracy of judgment of handwriting or composition.

Miss **Mulhall** said: Experiments were reported concerning, (1) the influence of determination to remember, and (2) the effect of primacy and recency on both recall and recognition. The results showed: (1) Determined recall (recall of material for which there was a determination to remember) differs from undetermined recall more than determined recognition differs from undetermined recognition. (2) The difference between determined recall and determined recognition is less than that between undetermined recall and undetermined recognition. (3) The factor of determination influences the amount of material remembered which can be associated with other material remembered. (4) Primacy and recency both influence recall memory. The influence of each on recognition is less than on recall, but is greater for material devoid of associations and less for material with associations. A detailed account of the experiments will appear in the forthcoming issue of the "American Journal of Psychology."

Mr. **Martin** said: The object of this investigation is to discover the transfer effects of practice in canceling *a-t* words upon certain other cancellation tests. The subjects were divided into two groups: thirty-six in the practice group and forty in the control group. Both groups were tested with a series of seven cancellation tests, after which the practice group was trained in canceling words containing *a* and *t* in English prose. The practice periods were ten minutes long and there were four of them each day for sixteen days. Precautions were taken to impel the practice group to a maximum of improvement, and also, in the meantime, to keep the remaining forty that constituted the control group interested in their part of the experiment. In the training series the practice group improved in accuracy from 83 per cent. to 96 per cent., and from an initial average performance of 10.2 cancellations per minute to a final average performance of 26.6 cancellations per minute. After the conclusion of the practice both groups were reassembled and tested with the same seven tests used before the practice began.

The results justify the following conclusions:

1). In the group of tests in which the elements determining the canceling were the same or partially the same as the elements determining the canceling in the practice series the transfer effects appear as facilitation.

2). In the group of tests in which there were none of the elements which determined the rate of canceling in the practice series the transfer effects are without appreciable or reliable manifestation.

3). In the group of tests in which the elements determining the canceling were among those to be neglected in the practice series, while the elements determining the canceling in the practice series were among those to be neglected in these tests the transfer effects appear as interference.

Dr. **Woodworth** said: Results cited from the literature and from the speaker's own experiments showed that in the main an influence which made for quickness of learning made also for good retention of the matter learned. But there were exceptions to this rule, the most important being that long lists of syllables, or other large masses of matter to be learned, though slowly learned, were strongly retained. This result has usually been explained by reference to the additional study given to the elements of the longer list because of their presence in the long list. An experiment was reported showing that this was not the full explanation. By the method of paired associates, lists of 5, 10, 20 and 30 pairs of unrelated English words were presented, each list receiving three readings, with test and prompting after each reading. The shorter lists were naturally more completely mastered in the three readings than the longer lists. Nevertheless, a test two days later showed that the pairs of the longer lists were much better learned than those of the shorter lists. From the lists of 5 pairs, 6 per cent. were retained; from the lists of 10 pairs, 15 per cent. were retained; from the lists of 20 pairs, 37 per cent. were retained; and from the lists of 30 pairs, 34 per cent. were retained. Retrospective notes by the 25 subjects indicate that length of list acts as a stimulus to effort, and that this effort goes to the discovery of meaningful connections between the members of a pair. Shortness of list favors quick rote learning, without much attention to meaning, while length of list favors meaningful apprehension, which in turn favors retention.

Dr. **Morgan** said: This paper was the report of an investigation intended to ascertain the effect of noisy conditions upon human activity. The procedure of the experiment consisted in having the subject work continuously at a task, the time for each step being recorded automatically. While thus working severe noises were introduced. Each subject worked for about one hour, a record being taken for the entire time.

The results show that: (1) When the disturbing noises were first introduced they caused a retardation in the speed of the work. (2) After the first slowing effect, the subject exceeded the speed he had made before

the disturbances were introduced. (3) After the removal of the disturbance the subject did slower work. (4) The records of errors do not show any inferior grade of work during the disturbance. (5) Since no index was obtained as to the amount of effort put forth by the subjects, these results throw no light on the favorability or unfavorability of the noisy conditions. They have a purely subjective intent, namely, that the subject is able to call forth enough extra energy to overcome any effect the noise may have.

Two attempts to get such an index were reported. One was by recording the involuntary difference in pressure that the subject exerted upon a dynamometer while at work. With an improvement in technique this method gives some promise. The other was to take a continuous respiration record. Measuring the time of each expiration and inspiration and finding the ratio between them (dividing the expiration by the inspiration) gives a means of comparing the different respirations numerically. In two experiments performed, this method gave definite results. They showed that this ratio increases as the subject begins work, and rises to a maximum. As he becomes accustomed to the work it drops somewhat. Noises cause a marked increase in the ratio, and removal of the disturbance a decrease. It is planned to ascertain whether future experimentation will corroborate these results.

The Section then adjourned.

R. H. LOWIE,
Secretary.

BUSINESS MEETING

1 MARCH, 1915

The Academy met at 8:15 P. M. at the American Museum of Natural History, President George F. Kunz presiding. In the absence of the Recording Secretary, Dr. Charles P. Berkey was appointed Secretary *pro tem*.

The minutes of the last business meeting were read and approved.

The following candidates for membership in the Academy, recommended by Council, were duly elected:

ACTIVE MEMBERSHIP

J. S. Lemon, Cosmos Club, Washington, D. C.,
Frank G. Gilbrith, 77 Brown Street, Providence, R. I.,
L. A. Adams, Columbia University.

The Secretary then reported the death, on 24 January, 1915, of Arthur Auwers, Honorary Member of the Academy since 1898.

The Academy then adjourned.

CHARLES P. BERKEY,
Secretary pro tem.

SECTION OF GEOLOGY AND MINERALOGY

1 MARCH, 1915

Section was called to order at 8:20 P. M., Vice-President Charles P. Berkey presiding, about twenty members and visitors being present. In the absence of the Secretary of the Section the minutes of previous meeting were not called for, and Mr. W. S. Smith was appointed Secretary *pro tem.*

There being no business to transact, the following scientific programme was offered:

Mrs. C. C. Mook,	A NEW CEPHALOPOD FROM THE SILURIC OF PENNSYLVANIA.
Miss Marjorie O'Connell,	CHARACTERISTICS OF A TYPICAL ESTUARY.
A. W. Grabau,	NEW LIGHT ON ANCIENT GEOGRAPHY FROM THE ROCKS AND FOSSILS OF MICHIGAN.

SUMMARY OF PAPERS

Mrs. **Mook** reported the finding of a specimen of *Trochoceras grovaniense* and exhibited the specimen. Dr. Grabau remarked on the importance of the contribution.

Miss **O'Connell** presented charts and maps to illustrate the importance of salinity on fauna, concluding that no such thing as a peculiar estuarine fauna existed. Miss O'Connell used the Baltic as an example of a typical estuary, a point that was questioned by Dr. Johnson, who was in turn answered by Dr. Grabau.

Dr. **Grabau's** paper was presented as a further step in a study already occupying some ten years. It included a development of the varying relations between land and water in Lower Siluric and succeeding periods, with particular light on the paleogeographic conditions in Monroan time as shed by recent studies of Michigan fauna. Many maps were used and a concise and extremely scientific summary was read. Dr. C. A. Reeds asked regarding sources of information.

The Section then adjourned.

WARREN S. SMITH,
Secretary pro tem.

SECTION OF BIOLOGY

8 MARCH, 1915

Section met at 8:15 p. m., Vice-President Raymond C. Osburn presiding.

The following programme was then offered:

L. A. Adams, PHYLOGENY OF THE MUSCLES OF MASTICATION IN VERTEBRATES.

SUMMARY OF PAPER

Mr. **Adams** said in abstract: The object of the investigation, which had been carried on at the American Museum of Natural History, was to discover the evolutionary history of the jaw muscles in vertebrates and to establish the homologies of the different elements throughout the vertebrate classes. While many anatomists had made intensive studies of the innervation of the muscles, very few had attempted to follow the muscles through the vertebrate classes, and no one had given an adequate series of figures. A series of 26 existing types of vertebrates had been carefully studied and figured, representing the Elasmobranchii, Chondrostei, Holostei, Teleostei, Crossopterygii, Dipnoi, Urodela, Anura, Chelonia, Rhynchocephalia, Lacertilia, Crocodilia, Aves and Mammalia. From the data thus obtained and by applying the principles that became apparent as the work proceeded, reconstructions of the jaw musculature were attempted in a series of extinct forms representing the Arthrodira, the Temnospondyli, the Cotylosauria, the Cynodontia and the Theropoda. The muscles under consideration fall under two main groups: first those innervated by the ramus mandibularis of the trigeminus nerve (here belong the temporalis, the masseter and the pterygoid muscles, as well as the tensor tympani), and secondly those innervated by the facialis nerve, including the posterior belly of the digastric, and in lower forms certain muscles of the hyoid and opercular regions. The first group is derived ultimately from the "adductor mass" in Elasmobranchs, the second from the hyoidean adductors (constrictor dorsalis 2), as held by Vetter and others.

The speaker illustrated the history of each of these groups in the different classes of vertebrates.¹

Dr. **W. K. Gregory**, in discussing Mr. Adams's paper, spoke of the bearing of these studies upon the morphology of the skull, especially in

¹ Mr. Adams' memoir on this subject has since been accepted for publication by the Academy.

reptiles. Exhibiting illustrations of the skull of the carnivorous dinosaur *Tyrannosaurus*, he showed how the superior and lateral temporal fenestræ appear to have served for the origin of the capiti-mandibularis muscle, while the pre-orbital fenestræ may have lodged the upper part of the pterygo-mandibularis.

The Section then adjourned.

WILLIAM K. GREGORY,
Secretary.

SECTION OF ASTRONOMY, PHYSICS AND CHEMISTRY

15 MARCH, 1915

Section met at 8:15 P. M., Vice-President Charles Baskerville presiding.

The minutes of the last meeting of the Section were read and approved.

The following programme was then offered:

A. W. Thomas,	THE ACTION OF DIASTASE ON STARCH.
W. G. Lyle, L. J. Curtman and	
J. T. W. Marshall,	A NEW TEST FOR COPPER.

SUMMARY OF PAPER

An abstract of the paper by Drs. W. G. Lyle, L. J. Curtman and Mr. J. T. W. Marshall is as follows: An aqueous solution of normal amino caproic acid was found to be an exceedingly sensitive reagent for the detection of copper. With this reagent 0.004 mg. of copper may be detected with certainty. Mercury and zinc are the only other common metals which yield under the conditions specified, a precipitate with the reagent. The interference of the former may be overcome by the addition of sodium chloride; the latter may be prevented from precipitating by adjusting the acidity of the solution. Procedures are given for the detection of small amounts of copper in the presence of relatively large quantities of foreign metals. The reagent is more specific for copper than any of the other reagents heretofore proposed and possesses an advantage over the ferrocyanide test, in that small quantities of iron do not interfere with its use.

The Section then adjourned.

E. E. SMITH,
Secretary.

SECTION OF ANTHROPOLOGY AND PSYCHOLOGY

22 MARCH, 1915

Under the auspices of the Section of Anthropology and Psychology, a general meeting of the Academy and its Affiliated Societies was held at 8:15 P. M., Professor R. S. Woodworth presiding.

The evening was devoted to the following lecture:

Raymond Dodge, INCIDENCE OF THE EFFECT OF MODERATE DOSES OF ALCOHOL ON THE NERVOUS SYSTEM.

SUMMARY OF PAPER

Professor **Dodge's** lecture gave an account of the principal neuromuscular techniques which were used in the first year of experimentation under the alcohol programme of the Nutrition Laboratory of the Carnegie Institution for a systematic study of the effects of moderate doses of alcohol on the human organism. These techniques were developed by many years of preliminary study to exclude arbitrary and voluntary modification of the data as far as possible, and gave a systematic view of nervous action at different levels.

The results of the experiments show that alcohol affects all levels of the nervous system, including the autonomic system, but in various degrees. The effect is greatest at those levels where the possibility of autogenic reinforcement is least. The relation between its effect on the cerebro-spinal and on the autonomic systems respectively indicates that alcohol decreases organic efficiency. The best indicator of the effect of alcohol on any particular individual appears to be its effect on the eye movements.

After the address a collation was served in the Eskimo Hall. This was followed by a reception to Professor Dodge, and the Section then adjourned.

R. H. LOWIE,
Secretary.

BUSINESS MEETING

5 APRIL, 1915

The Academy met at 8:15 P. M. at the American Museum of Natural History, President George F. Kunz presiding. In the absence of the Recording Secretary, Dr. Charles P. Berkey was elected Secretary *pro tem*.

The minutes of the last business meeting were read and approved.

The following candidate for Active Membership in the Academy, recommended by Council, was duly elected:

Victor Emanuel Levine, College of Physicians and Surgeons.

The Secretary reported the death of Francis Hustace, Active Member of the Academy since 1907.

The Academy then adjourned.

CHARLES P. BERKEY.

Secretary pro tem.

SECTION OF GEOLOGY AND MINERALOGY

5 APRIL, 1915

Section was called to order immediately after the adjournment of the regular meeting of the Academy, Vice-President Charles P. Berkey, presiding.

The resignation of the Secretary, Dr. A. B. Pacini, was accepted, and Professor D. W. Johnson was elected to serve out the unexpired term.

The following programme was offered:

W. S. Smith, AREAL AND ECONOMIC GEOLOGY OF SKYKOMISH BASIN,
WASHINGTON.

SUMMARY OF PAPER

Mr. **Smith** described the topography of the Skykomish district in the Cascade Mountains and briefly explained the geological history of the region. Special emphasis was laid upon the relationship of the different batholithic intrusions which occupy a large part of the area under discussion. The paper was illustrated by a geologic map, photographs and numerous rock specimens, and was discussed by D. W. Johnson, C. A. Reeds and C. C. Mook.

D. W. JOHNSON,

Secretary.

SECTION OF BIOLOGY

12 APRIL, 1915

Section met at 8:15 P. M., Vice-President Raymond C. Osburn presiding.

The following programme was then offered:

Henry Fairfield Osborn, MEN OF THE OLD STONE AGE.

REVIEW OF THE PLEISTOCENE OF EUROPE,
ASIA AND NORTHERN AFRICA.² (Read by
title.)

J. H. MacGregor,

NEW RESTORATIONS OF PREHISTORIC MEN:
PITHECANTHROPUS, PILTDOWN, NEANDERTHAL,
CRO-MAGNON.

SUMMARY OF PAPERS

Professor **Osborn** summarized the chief results of his synthetic work on the early history of man in Europe, in which he had enjoyed the coöperation of many archaeologists, anatomists and geologists. He outlined the geological, climatic and faunal history of Europe during the Pleistocene, with special reference to the palæolithic stages, exhibiting a large chart, which had been prepared in collaboration with Dr. C. A. Reeds, illustrating the successive advances and retreats of the glaciers and the corresponding succession of mammalian faunas and races of man.

Illustrations of the skeletal remains of the palæolithic races were passed in review and the chief characters of each race noted.

Professor **MacGregor** exhibited his remarkably life-like series of busts of prehistoric men and a corresponding series of skull models, which had been reconstructed from casts of the original specimens. The skull reconstructions had been made with careful consideration of all available evidence from comparative anatomy and palæontology. After completing each skull model, the flesh was restored at many points, the thickness being determined from the well known results of dissection of recent human subjects.

The facial characteristics of each race, so far as they could be inferred from the skull structure, were described.

Doctor Hrdlicka, in discussing the papers of Professors Osborn and MacGregor, held that the La Ferassie remains were intermediate in character between *Homo neanderthalensis* and *H. sapiens* and indicated a transition from one to the other.

Professor Osborn, in reply, expressed his opinion that the Neanderthaloids were not ancestral to the higher type.

The Section then adjourned.

WILLIAM K. GREGORY,
Secretary.

² Published in the Annals, Vol. XXVI, pp. 215-315, 30 July, 1915.

SECTION OF ANTHROPOLOGY AND PSYCHOLOGY

19 APRIL, 1915

Section met in conjunction with the New York Branch of the American Psychological Association at Columbia University, Professor R. S. Woodworth presiding.

The following programme was offered:

G. O. Ferguson,	RELATIVE PERFORMANCE OF NEGROES AND WHITES IN SOME MENTAL TESTS.
Robert A. Cummins,	DISTRIBUTION OF TIME IN SCHOOL EXERCISES.
H. A. Ruger,	REPORT ON EXPERIMENTS WITH THE HAMPTON COURT MAZE.
M. R. Trabue,	COMPLETION TESTS WITH PUBLIC SCHOOL CHILD- DREN.
Mark A. May,	AN EXPERIMENTAL STUDY IN VALUES.
Will S. Monroe,	THE STUDY OF FOREIGN LANGUAGES IN RELATION TO STANDING IN PSYCHOLOGY.
L. H. Horton,	SCIENTIFIC METHOD IN THE INTERPRETATION OF DREAMS.
Gary C. Myers,	STUDIES IN RECALL.

SUMMARY OF PAPERS

Mr. **Ferguson** said in abstract: Tests were made upon 486 white and 421 colored pupils in the grammar and high-school grades of Richmond, Fredericksburg and Newport News, Virginia. In the Woodworth and Wells "Mixed Relations" test, and in the Trabue "Completion" test, the colored children scored approximately three fourths as high as the white children; in the "Columbia Straight Maze" test there was no appreciable racial difference in ability; in a cancellation test the colored girls were slightly superior to the white girls, and the colored boys did as well as the white boys.

The colored pupils were divided into four classes on the basis of racial purity as indicated by skin color, hair texture, and facial and cranial conformation. In the mixed relations and completion tests, the pure negroes, the negroes three fourths pure, the mulattoes, and the quadroons scored respectively as follows: approximately 60, 70, 80 and 90 per cent. as high as whites.

The variability of the colored pupils as a whole was fully as great as that of the whites, likewise the variability of the mulattoes. But the pure

negroes, the negroes three fourths pure, and the quadroons were somewhat less variable than the whites. The results of the experiments will be published in full in the "Archives of Psychology."

Professor **Cummins** said in abstract: The investigation concerns the practical application of the laws of memory in such public-school exercises as geography and history, and deals with the relative advantages of an irregular distribution of time as compared with the regular distribution which is commonly used in the arrangement of the school programme.

Subjects.—The subjects used in the experiment included pupils in grades from the third to the seventh—a total of 699.

The seventh-grade pupils were in the Rutherford, New Jersey, public school and were mostly Americans of good social standing. Those of the other grades were from the Lyndhurst, New Jersey, public schools and represented about 50 per cent. of foreigners, mostly Italians and Pollocks, being of a rather low grade of economic and social standing.

Materials.—The standard one-column addition sheets of Thorndike were used with the third and fourth grades: the division sheets devised by Kirby were used in the fifth grade: in the upper grades the geography and history material used was devised by the writer and consisted of a selection of principles and facts of geography condensed into brief sentences and printed on sheets 6 x 9 and 6 x 12 inches. These sheets were passed out for study. These, after a given length of time, were taken up and other sheets passed out. These latter sheets were the same as the first ones except that all the important words were omitted and the numbers, which, by the way, were placed in parentheses in front of these words on the study sheets, indicated the missing words. The pupils were required to write on separate scoring sheets as many of these missing words as possible in a given time.

Task.—The task assigned in all the grades consisted in doing the exercises in addition, division, geography or history, as the case might be, so many minutes, say 5, 10, or 15, per day or per every other day, or what not, according to the arrangement of the time schedule for each group. A total of 115 minutes was used with the third and fourth grades doing addition. The same time was used with the fifth grade doing division, the measurement being taken from the mid-point of the initial fifteen minutes of practise to the mid-point of the final fifteen minutes of practise—i. e., 100 minutes of practise were measured. In the case of the sixth and seventh grades doing geography and history a total of 120 minutes was used in the experiment, the measurement being taken from the mid-point of the initial fifteen minutes of practise to the mid-point of the final fifteen minutes of practise—i. e., 105 minutes of practise were measured.

Distribution of time.—Several different schedules of time distribution were carried out, which can not be described here in detail, but suffice it to say that the main comparison was made between a regular distribution—i. e., 15, 15, 15, etc., or 10, 10, 10, etc.—per day, or per every other day, as the case might be, with an irregular distribution—i. e., 15, 15, 10, 10, 5, etc.—or a decreasing number of minutes and an increasing time-interval between the periods of practise.

Time of day.—No special effort was made to keep the time of day constant. Some classes worked in the afternoon and some in the forenoon. A check was kept on this and no appreciable difference seems to be manifest by this factor.

Stress.—In the beginning it was aimed to stress accuracy at least enough to keep up to the standard set in the initial practise and if possible to show a consistent gain in same. This was done.

Conductors of the experiment.—The writer personally conducted all the initial and final practises, the entire experiment with the sixth and seventh grades and practically all the work with the lower grades. In a few instances it was impossible because of lack of time to get around to all the sections at the time appointed, and in such cases the teacher took charge of the practise. All the teachers were in the rooms during all the work and consequently were able to take charge without any change in either the stress or the method.

Conclusion.—The results show an improvement of about 50 per cent. in addition, 100 per cent. in division and from 50 to 150 per cent. in geography and history, with a noticeably larger increase in case of the groups working according to the irregular distribution of time. In point of accuracy there was an increase of 1 to 9 per cent. in all cases. The experiment seems to warrant the conclusion that an irregular distribution of time is more advantageous in the case of such school subjects as are here considered.

Mr. **Trabue** said in abstract: After testing over six thousand public-school children with a series of fifty-six mutilated sentences, twenty-four of the sentences were selected to serve as a language scale.³

Sentences were used rather than paragraphs, because it was believed that the paragraph was too large a unit of thought for the child in the lower grades to handle successfully. The mental labor required of the teacher in evaluating paragraph completions has heretofore kept teachers from making much use of completion tests. The short sentence units here presented to the child for completion and to the teacher for evalua-

³ Cf. M. R. Trabue: "Some Results of a Graded Series of Completion Tests." *School and Society*, Vol. I, pp. 537-540.

tion seemed to eliminate many of the objections which have been brought against the use of completion tests with public-school children.

Since it was desired to test the child's ability to think about and to use intelligently the ordinary words of the English language, the subject-matter of the sentences was taken from general experience and human relations, avoiding in so far as possible the more specialized fields of knowledge.

An elaborate scheme of evaluated completions was at first followed in scoring each sentence, giving five points score to each perfectly completed sentence, four points to each sentence only slightly imperfect, three points to each sentence containing a more serious error, two points to a very imperfectly completed sentence and one point if the sentence showed any evidence whatever that the child had understood the printed words. The present scheme of scoring gives two points score where five were originally given, one point where four or three were given and no score at all where two or one were at first assigned.

That the present method of scoring is practically as reliable as the older, more elaborate method is indicated by the fact that the fifty-six sentences tend to hold their relative rank regardless of which method is used. The rank obtained by testing fifty-seven pupils in the last half of the eighth grade showed a correlation (Spearman's method of squared differences) of .965 with the rank obtained from testing thirty-four pupils in the first half of the sixth grade, when the older method of scoring was employed, while with the newer method of scoring, $r = .9623$. The ranks obtained by the two methods from the fifty-seven pupils in the eighth grade gave a correlation of .9823, and with the thirty-four pupils in the sixth grade, $r = .9768$. Such small differences between the two methods of scoring the tests were not thought sufficient to warrant the enormous amount of additional labor required to score the sentences by the old, more elaborate scheme.

Since each of the twenty-four sentences of Language Scale A may receive two points credit, the maximum score is forty-eight points. The average scores in Language Scale A of over five thousand children in three different school systems are given below by grades, the P.E. of any grade average being 3.5 points.

School grade...	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII
Av. score.....	3.4	7.7	12.1	16.2	19.5	22.5	26.4	28.9	32.9	34.8	37.3

Mr. May said in abstract: The work here reported represents a preliminary attempt to apply the order of merit method to the study of "religious values." The materials used for the experiment were twenty-

five religious situations, the most of which are found in any order of worship of Protestant churches. The subjects were asked to imagine themselves in each of these situations and then to arrange them in the order of their merit for pure pleasure. After this arrangement had been made, they were asked to arrange the same material a second time for its religious value—religious value being defined as “communion with God.” Then still a third arrangement was made for moral value. Fifty students in Union Theological Seminary judged this material in each of these three ways.

The most significant features of the investigations may be summed up under the following heads:

1). The fact that fifty judges judged these situations without complaining that it could not be done would seem to indicate that if a sufficient number of competent judges could be obtained it would be possible to derive a scale for measuring the relative values of religious and moral situations.

2). By having the same material judged according to three different criteria we are able to analyze a given situation and to determine its moral, religious and æsthetic value.

3). The experiment shows that on the whole this is a very satisfactory method of defining and bringing out of obscurity what we mean when we talk in such vague terms about the “values of life.”

Mr. **Horton** said in abstract: The question here considered is whether dream interpretations shall represent the state of the dreamer's mind or the mere fancy of the interpreter. Criticism is directed at the aprioristic and oftentimes hit-or-miss practises of the Vienna and Zürich schools of psychoanalysis.

For illustration, a simple dream is interpreted by the current methods of psychoanalysts. First, according to the “reductive method” of Freud, it is made out as symbolizing an infantile and sexual wish-fulfilment, expressing a “*royeur*” component of the *Libido*. Secondly, the dream is reinterpreted by Jung's “constructive method,” so as to gloss over the gross Freudian phallicism. It is now made to mean that the dreamer is impelled to higher biological duties, namely, marriage and professional success.

The plausibility of these interpretations once shown, they are next proved wide of the mark, by the fact that the dream can be more adequately accounted for in another way—*i. e.*, by a proposed “reconstitutive method.”

This method aims to “reconstitute” the dream-thought (both imaged and imageless) by tracing the wave of nervous excitation from its origin

in a primary stimulus-idea through a specific apperception-mass into a derived system of secondary images which form the manifest dream content. The derivation of the latter must be concretely demonstrated in the "settings of ideas"—not assumed.

The reconstitution of this particular dream illustrates the *reductio ad absurdum* of the two previous psychoanalytic "solutions." The fact that either of them would apparently have satisfied the demands of the problem is an artifact evolved by the interpreter's confabulations and forcing of analogy. It is a matter of "will to interpret."

The Freudian technique is unsound in so far as it fails to consider the meaning of dream-items as determined by "unconscious settings of ideas."

The study of individual differences in dreams indicates that the supposed "language of dreams" is an artifact; that the psychic "censorship" is only an occasional phenomenon. The reconstitutive method brings into relief the trial-and-error character of the dreaming process, depicting the organism as attempting a physiological resolution of persisting and unadjusted stimulus-ideas. The images evoked in the dream have the psychological character of "trial percepts" or tentative apperceptions.

Sleep favors apperceptive errors; hence the inconsistency and bizarrerie of the dream. The significance of a dream can be found only by reconstituting it from the above standpoint.

Dr. Myers said in abstract: Two experiments in progress were reported—Reconstructive Recall and Confusion in Recall. In the first experiment the subjects daily tried to recall as much as possible of certain selections which they once knew very well, but which they had forgotten wholly or in part. The subjects wrote introspections. Several times as much was reconstructed at the end of a few weeks as the amount reproduced in the first recall. Interesting chains of associations were obvious. Paragraphs and sentences mutilated or entire were recalled and improved upon or linked with others in subsequent recalls.

The results thus far endorse the common statement of psychologists, "We never wholly forget," and they emphasize the importance of the most favorable situations to elicit the learner's reproduction. They suggest a prominent existence of subliminal association, and, most of all, a serious neglect in almost all memory experiments to consider the time for recall as a factor in measuring memory, and, in case of group experiments, to provide any time limit for recall.

In the second study the purpose is to determine the increase of confusion with the increase of retention interval. The following test is used:

273	732	372	723
beat	tow	desert	waist
statue	meat	week	pear
dessert	waste	stake	toe
steak	kernel	beet	meet
weak	pair	statute	colonel

The subjects are told to study the materials, so as to be able to reproduce the correct words under their respective numbers. A hundred subjects, tested individually, were told to study until they were sure they could give perfect reproduction. Their times for learning and for recall were kept. They were surprised by a request for a second recall after three weeks. Five minutes for learning and three minutes for recall were allowed 278 public-school children tested. They were surprised by a second recall after one day and a third recall five weeks later.

Partial results of the latter group only were presented. The average percentage of the correct words and figures that are recalled in correct order is used to measure the amount of absence of confusion. By the 159 boys and girls of the high school the average per cent. for words in immediate recall is 71.3 and after one day 60.9. For figures the percentages are 74.4 and 70.4. By the eighth grade the records are: Words, 78.8 and 62.9; figures, 73.8 and 51.5. Seventh grade: Words, 56.1 and 39.7; figures, 53.3 and 27.4. Sixth grade: Words, 60.0 and 43.7; figures, 61.9 and 49.6. This shows confusion in the first recall and a very pronounced increase in confusion after one day.

The Section then adjourned.

R. H. LOWIE,
Secretary.

SECTION OF ASTRONOMY, PHYSICS AND CHEMISTRY

26 APRIL, 1915

Under the auspices of the Section of Astronomy, Physics and Chemistry, a general meeting of the Academy and its Affiliated Societies was held in the main lecture hall at the American Museum of Natural History at 8:15 P. M., President George F. Kunz presiding.

The following lecture was presented:

Arthur L. Day, THE VOLCANO KILAUEA IN ACTION.

SUMMARY OF PAPER

Dr. **Day** said in abstract: This work is concerned chiefly with the identification of and the reactions between the gaseous ingredients set free by

the liquid lava at Kilauea during the summer of 1912. A successful attempt was made to collect these gases directly from the liquid lava at a temperature of 1000° before they reached the atmosphere. The collection of the gas before it has become altered by combustion with air has proved to be an insurmountable difficulty hitherto, whether the gases were collected in tubes for analysis in the laboratory or studied at the point of emergence with the spectroscope. In either case, the gases were burned or were in process of combustion, and therefore could not reveal either the true identity or the original relation of the gases participating in volcanic activity below the surface. This is the first time that unaltered volcano gases have ever been obtained for study.

In so far as the present reconnaissance yields final results, it shows that the gases evolved from the hot lava at the Halemaumau crater are N_2 , H_2O , CO_2 , CO , SO_2 , free H and free S; with Cl, F and perhaps NH_3 in comparatively insignificant quantity. No argon was found, nor any of the other rare gases.

The main conclusion, upon finding this group of gases in association at 1000° or higher, is that they cannot be in equilibrium at that temperature and must be in process of active reaction among themselves; there can be no equilibrium, for example, between free sulphur and CO_2 , nor between free hydrogen and SO_2 or CO_2 .

This is a conclusion of rather far-reaching consequence, for it must mean that the relative proportions of the gases are constantly in process of local change—a fact which is supported by the very considerable differences between the analyses of the gases contained in different tubes which were filled at the same time. Since these reactions are strongly exothermic, it also follows that a very large and constantly increasing amount of heat is set free during the rise of the gases to the surface. In support of this it was also observed that when the quantity of gas set free was large the temperature of the liquid lava in the basin was higher (July 6, 1912, 1185°); when the amount of discharged gas was small it was lower (June 13, 1912, 1070°), the quantity of lava in the basin remaining substantially the same.

Controverting a view recently put forth, H_2O was found to be present as such among the gases set free, as indeed it inevitably must be, for it has long been known that free hydrogen in association with SO_2 and CO_2 will react to form water at these temperatures.

Neither hydrocarbons nor chlorine in appreciable quantities were found.

After the address, a collation was served in the Eskimo Hall. This was followed by a reception to Dr. Day, and the Section then adjourned.

E. E. SMITH,

Secretary.

BUSINESS MEETING

3 MAY, 1915

The Academy met at 8:20 P. M. at the American Museum of Natural History, President George F. Kunz presiding. In the absence of the Recording Secretary, Professor J. F. Kemp was appointed Secretary *pro tem*.

The minutes of the last business meeting were read and approved. The Academy then adjourned.

J. F. KEMP,
Secretary pro tem.

SECTION OF GEOLOGY AND MINERALOGY

3 MAY, 1915

Section met at 8:25 P. M., Vice-President Charles P. Berkey presiding. In the absence of the Secretary, Professor J. F. Kemp was appointed Secretary *pro tem*.

The minutes of the last meeting were read and approved.

The following programme was offered:

George I. Finlay, THE ICE FIELDS OF PRINCE WILLIAM SOUND.
C. C. Mook, A STUDY OF THE MORRISON FORMATION.

Dr. **Mook's** paper was discussed by Professors Kemp and Finlay. The Section then adjourned.

J. F. KEMP,
Secretary pro tem.

SECTION OF BIOLOGY

10 MAY, 1915

Section met at 8:15 P. M., Vice-President Raymond C. Osburn presiding.

The following programme was then offered:

C. H. Townsend, REPORT ON THE WORK OF THE UNITED STATES FISHERIES STEAMER "FISH HAWK" IN THE WESTERN END OF LONG ISLAND SOUND IN THE SUMMER OF 1914.

Raymond C. Osburn, THE GEOGRAPHIC DISTRIBUTION OF THE BRYOZOA OF THE ATLANTIC COAST OF NORTH AMERICA.

Dr. **Townsend** exhibited motion pictures of the recent biological survey work of the "Fish Hawk" in the Long Island Sound. Dredging apparatus and methods were illustrated. The fauna of the muddy bottom in the middle of the Sound was also illustrated and described. It includes great numbers of spider-crabs, flounders and whelks and differs from the fauna of the margins, where oyster-beds abound.

Dr. **Charles B. Davenport**, director of the Carnegie Station for Experimental Evolution at Cold Spring Harbor, Long Island, described the fauna of the brackish waters on the north shores of Long Island; here are to be found, along with fresh-water forms, a number of salt-water animals, such as mussels, *Littorina* and barnacles, which can live in brackish water only when they can get purer salt water at high tide.

Professor **Raymond C. Osburn** said in abstract: Nearly 300 species of Bryozoa are known to inhabit the coastal shelf, down to the 100-fathom line. The species fall for the most part into three groups: 1. cosmopolitan species, or those of wide range; 2. northern species, often circumpolar, which range southward along the coast, and 3. tropical species, which range northward from Florida. Species of limited distribution also occur here and there along the coast.

According to orders and distribution, the species may be arranged in the form of a table:

	Endo- procta	Cyclo- stomata	Cteno- stomata	Cheilo- stomata	Total
Canada and northward.....	3	10	1	28	42
Canada and ranging south to Cape Cod	3	7	3	66	79
Canada and ranging south to Cape Hatteras	0	0	0	7	7
Canada and ranging south to Florida.	1	4	1	12	18
Cape Cod to Florida.....	1	0	1	5	7
Cape Hatteras to Florida.....	2	2	1	21	26
Florida	2	5	2	70	79
Cape Cod to Cape Hatteras.....	0	0	4	3	7
Cape Cod.....	2	0	3	2	7
Cape Hatteras.....	2	1	3	3	9
Totals.....	16	23	19	216	291

As the above groups are mutually exclusive, this gives a fair idea of the distribution of the several orders.

The total number of species found in each region of the coast is as follows:

Known from eastern Canada.....	128
Known from eastern New England, including Cape Cod.....	124

Known from Cape Cod to Cape Hatteras, inclusive.....	122
Known from Cape Hatteras and south to Florida.....	139
Known from Florida.....	130

It will thus be seen that there is a fairly even distribution along the coast, although locally, of course, some regions will be found much richer than others.

Species of the north may run into well-marked varieties in the south, and *vice versa*. Also northern species of the shallow waters may be found only in deeper waters to the southward. Two well-marked barriers present themselves along the coast, viz., Cape Cod and Cape Hatteras. North of Cape Cod the fauna is typically northern, while south of Cape Hatteras it is tropical. Less than 20 species from south of Hatteras range from south of Cape Hatteras to Cape Cod.

Charts indicating the distribution of temperatures at the surface in summer and winter and at 100 meters, a current chart and numerous species of Bryozoa were shown by means of the lantern.

The Section then adjourned.

WILLIAM K. GREGORY,
Secretary.

BUSINESS MEETING

17 MAY, 1915

The Academy met at 5:44 P. M., at the American Museum of Natural History, Vice-President Clark Wissler presiding.

The minutes of the last business meeting were read and approved.

The following candidate for Associate Membership in the Academy, recommended by Council, was duly elected:

R. J. Colony, Cooper Union Institute.

The Recording Secretary reported the death on 22 March, 1915, of Dr. A. A. Hubrecht, Honorary Member of the Academy since 1896.

The Academy then adjourned.

EDMUND OTIS HOVEY,
Recording Secretary.

BUSINESS MEETING

4 OCTOBER, 1915

The Academy met at 8:15 P. M., President George F. Kunz presiding.

In the absence of the Recording Secretary, Professor D. W. Johnson was appointed Secretary *pro tem*.

The minutes of the last meeting were read and approved.

There being no further business to transact, the Academy then adjourned.

D. W. JOHNSON,
Secretary pro tem.

SECTION OF GEOLOGY AND MINERALOGY

4 OCTOBER, 1915

Section met at 8:20 P. M., Vice-President Charles P. Berkey presiding.

The minutes of the last meeting of the Section were read and approved.

The following programme was then offered:

R. J. Colony, PETROGRAPHIC METHODS APPLIED TO THE STUDY OF CEMENT.

SUMMARY OF PAPER

Mr. Colony said in abstract: In a previous paper (Petrographic study of Portland cement; School of Mines Quarterly, 5-XXXVI, 1914) the character of cement clinker has been briefly discussed from a petrographic standpoint, and the fact emphasized that while the components of the clinker, Alit, Belit and Celit, have a mineral identity, they are, individually, complex solid solutions composed of two or more components each; these solid solutions may vary within the limits of solubility of the solute in each case, and it seems quite likely that such variability may affect the resulting cement.

It was also pointed out that when cement is gaged with water the first products of the reaction which follows are primary crystalline calcium hydrate with spherulitic habit; a multitude of minute, formless isotropic grains judged to be hydration products, and a greater or less amount of primary colloid of uncertain composition which co-precipitates with the spherulitic calcium hydrate, the resulting structure being minutely lamelloid. A secondary reaction then takes place between these components, which form a dense, structureless constituent, called the amorphous constituent proper.

It was also stated that secondary calcium hydrate which later forms in various situations, especially in voids and cavities, was hexagonal, uniaxial and optically negative.

Further study of numerous thin sections of cement and concrete, in

some of which this component appeared in particularly favorable development, proves calcium hydrate to be pseudo-hexagonal and pseudo-uniaxial. It is actually biaxial, with a very small optic angle, possesses good basal cleavage, and is probably monoclinic in crystallization, being strikingly similar to the micas in form.

It seems to be further demonstrated that the amorphous constituent itself is variable in character, differing in different cements, and the departure from what may, for the moment, be called the normal, is apparently a function of its inability to resist the action of agents of disintegration; this interpretation is tentative, however, pending further investigation. It follows, from this, that the amorphous constituent should be interpreted with caution, the mere fact of its presence not being sufficient to indicate that the cement in question would be suitable for use in situations exposed to the action of water.

It also seems apparent that the character and development of this constituent is affected by the quantity of water used in making the concrete, and possibly by other factors not yet determined, so that its formation may be partially or even completely suppressed, leaving relatively large amounts of primary crystalline calcium hydrate unchanged—a condition which renders the concrete extremely susceptible to the action of various agents of disintegration.

Defective concrete, taken from actual structures, the disintegration of which was traced to this cause, was briefly discussed.

The paper proved of exceptional interest and elicited much favorable criticism. Dr. George F. Kunz, Mr. Nathan Johnson, Mr. Charles Hoadley, Mr. Benjamin Howes, Professor I. H. Ogilvie, Mr. F. K. Morris, Professor G. I. Finlay and Professor C. P. Berkey participated in a discussion to which more than thirty-five contributions were made.

The Section then adjourned.

DOUGLAS W. JOHNSON,
Secretary.

BUSINESS MEETING

11 OCTOBER, 1915

The Academy met at 5:30 P. M. at the American Museum of Natural History, President George F. Kunz presiding. In the absence of the Recording Secretary, Dr. H. E. Crampton was appointed Acting Recording Secretary.

The minutes of the last business meeting were read and approved.

The following candidates for membership in the Academy, recommended by Council, were duly elected:

ACTIVE MEMBERSHIP

P. Maxwell Foshay, 34 Nassau Street,
A. J. Goldfarb, College of the City of New York,
Hermann J. Muller, Columbia University;
J. Leon Williams, 220 West 42nd Street.

The Acting Recording Secretary reported the following deaths:

James C. Fargo, Active Member of the Academy since 1878, died 8 February, 1915,

Thomas H. Hubbard, Life Member of the Academy since 1905, died 19 August, 1915,

Albert Plaut, Active Member of the Academy since 1910, died 17 June, 1915,

Samuel Thorne, Active Member of the Academy since 1899, died 4 July, 1915,

Charles T. Wills, Active Member of the Academy since 1897, died 31 August, 1915.

The Academy then adjourned.

HENRY E. CRAMPTON,
Acting Recording Secretary.

SECTION OF BIOLOGY

11 OCTOBER, 1915

Section met at 8:15 P. M., Professor H. von W. Schulte presiding. The following programme was then offered:

A. J. Goldfarb, EXPERIMENTALLY GRAFTED ORGANISMS: A REPORT OF RECENT RESEARCHES.

Professor **Goldfarb** said in abstract: The work of Roux, Morgan, Driesch and others has raised numerous problems relating to the production of half embryos from half eggs, half-size embryos, giant embryos and other abnormal forms. Since 1910 the speaker had been experimenting with sea-urchin eggs. By dissolving off the fertilization membrane and bringing the eggs into contact, fusion had taken place in varying degrees, ranging from slight adhesion to complete union of two eggs into one. From such more or less united eggs develop larvæ that lack certain

parts. Close examination of the anatomy of these larvæ usually reveals the character and extent of the fusion of the eggs that produced them. In general the extent of the morphological disturbance in experimentally grafted organisms was proportional to the area of the surfaces brought into contact.

The paper was discussed by Doctors Uhlenhut, Riddle, Pike and Schulte.

The Section then adjourned.

WILLIAM K. GREGORY,
Secretary.

SECTION OF ASTRONOMY, PHYSICS AND CHEMISTRY

18 OCTOBER, 1915

Section met at 8:15 P. M., Vice-President Charles Baskerville presiding.

The minutes of the last meeting of the Section were read and approved.

The following programme was then offered:

J. C. Olsen, ELECTROLYTIC METHOD OF SEWAGE DISPOSAL.

H. V. Army, STANDARDIZED COLORED FLUIDS.

SUMMARY OF PAPERS

Professor **Olsen** said in abstract: The method described has been in operation at Elmhurst, Borough of Queens, City of New York, for about a year and a half. An experimental apparatus of 25,000 gallons daily capacity was first installed and tested. The results were so satisfactory that a half million gallon unit was installed and has been in operation for about six months.

The machine contains over a thousand iron plates which act as electrodes. The sewage passes in thin sheets between the plates. Rotating paddles between the plates serve to remove any deposits which may form and short circuit the current. The current used is about 30 amperes and 80 volts.

The sewage first passes through a one-fourth inch screen, then through the electrolytic machine, after which milk of lime is added. It then passes through four sedimentation tanks.

The electrolysis produces about 2 c. c. of anodic oxygen per liter of sewage. This oxygen acts upon the dissolved organic matter in the sewage. The current also precipitates colloidal matter dissolved in the sewage. When the lime is added to the electrolyzed sewage, heavy flocks are

produced which consist of lime and organic matter. After the precipitated matter has been allowed to settle, an effluent is obtained which is clear, colorless and free from suspended matter. The bacterial content is low, generally only a few hundred, and decreases on standing. The dissolved oxygen is high and very rapidly rises to about 80 per cent. There is no odor whatever, the effluent being entirely stable and suitable for discharge into any stream. There is no odor or nuisance whatever about the plant, which may be placed at any sewer outlet. About one-half ton of lime is used per million gallons of sewage, the cost of lime and electric current being about \$10 per million gallons of sewage.

Professor **Army** gave a demonstration consisting of an exhibition of three sets of standard colored fluids, designated as the "Co-Fe-Cu," the "Co-Cro-Cu" and the "Cro-Manganate" blends.

The "Co-Fe-Cu" tints have as their basis red acidulated half-normal cobalt solution containing 59.49 grammes of cobalt chloride $\text{CoCl}_2 \cdot 6\text{H}_2\text{O}$ to the liter, the solvent being 1 per cent. hydrochloric acid; yellow acidulated half-normal ferric solution, containing 45.05 grammes of ferric chloride $\text{FeCl}_3 \cdot 6\text{H}_2\text{O}$ to the liter, the solvent being 1 per cent. hydrochloric acid and blue acidulated half-normal copper solution containing 62.43 grammes of copper sulphate $\text{CuSO}_4 \cdot 5\text{H}_2\text{O}$ to the liter, the solvent being 1 per cent. hydrochloric acid.

The "Co-Cro-Cu" tints are prepared from ammoniacal solutions of the three elements mentioned, the solvent in each case being 2.8 per cent. ammonia water. These consist of red ammoniacal fiftieth-normal cobalt solution containing 2.7 grammes of roseo-cobaltic chloride $\text{CoCl}_3 \cdot 5\text{NH}_3 \cdot \text{H}_2\text{O}$ to the liter; yellow ammoniacal fiftieth-normal chromium solution containing 0.420 grammes of ammonium dichromate $(\text{NH}_4)_2\text{Cr}_2\text{O}_7$ to the liter; blue ammoniacal fiftieth-normal copper solution containing the equivalent of 2.496 grammes of copper sulphate to the liter. Details concerning the preparation of these "Co-Cro-Cu" fluids and their blends will be found in an article by H. V. Army and C. H. Ring in the Journal of the Franklin Institute for August, 1915.

The blending of the acidulated fluids to make the "Co-Fe-Cu" tints and of the ammoniacal fluids to make the "Co-Cro-Cu" hues can, of course, be performed in any proportion that fancy suggests. The 91 samples of each series which were exhibited included the possible blends produced in making 12 c. c. of finished fluid when the ingredients are mixed in even (non-fractional) cubic centimeter quantities. The nomenclature devised is of the simplest kind. Thus the original red fluid is "R.Y.B. 12-0-0," the original yellow is "R.Y.B. 0-12-0" and the original blue is "R.Y.B. 0-0-12." The sample designated as "R.Y.B. 6-6-0" will,

of course, be an orange hue; that called "R.Y.B. 0-6-6" will be green, while "R.Y.B. 6-0-6" has a purplish hue.

That the intensity of color of each of the three basic fluids is about the same is shown by the fact that "R.Y.B. 4-4-4" closely approached both in the "Co-Fe-Cu," and in the "Co-Cro-Cu" series the "neutral gray," which is the nearest that blended reds, yellows and blues, can approach to pure white in solids or transparent colorlessness in fluids.

As to the permanency of these fluids, the original acidulated cobalt, iron and copper solutions and their blends neither fade nor precipitate to a perceptible degree until at least two years old; the ammoniacal cobalt and chromium solutions have now been under observation for over a year without any fading being detected. The ammoniacal copper, on the other hand, unless kept sealed, precipitates and consequently undergoes color change after a few weeks. However, the ammoniacal copper solution is in practice prepared extemporaneously by diluting the permanent half-normal acidulated copper solution to fiftieth-normal strength by addition of ammonia water and water, hence the preparation of the "Co-Cro-Cu" blends is merely a matter of mixing solutions that can be kept in stock for months without deterioration.

As to the practical application of these fluids, it has been found that in a properly conducted Nessler test an ammonia dilution representing a nitrogen content of 1 to 500,000 matched the "Co-Fe-Cu" blend 3-9-0, when this half-normal mixture was diluted to "50 per cent" of its original strength by addition of an equal volume of water; that the color of the phenol-sulphonic acid test for nitrates, when the nitrogen content was 1 in 500,000, was matched by "Co-Fe-Cu" blend 0-12-0 when this was diluted to "66 per cent." strength; that the molybdate assay for phosphoric acid, 1 in 20,000, gave a yellow color exactly matched by "Co-Cro-Cu 0-12-0" diluted to "15 per cent." strength; that Folin's vanillin test, when the vanillin content was 1 in 100,000, gave a color matched by "Co-Cro-Cu" blend 3-3-10; that Riegler's uric acid test of a uric acid content of 1 in 40,000 had the same tint as "Co-Cro-Cu" blend 2-2-8, and that a salicylic acid dilution of 1 in 50,000, when treated with the proper amount of ferric chloride solution, produced a color exactly matching "Co-Cro-Cu" blend 7-1-5 that had been diluted to 65 per cent. strength.

The two sets of colored fluids "Co-Fe-Cu" and "Co-Cro-Cu" fail when it comes to certain shades of red. Thus the color produced in the naphthylamine-sulphanilic acid test for nitrites had no match in the pink fluids of the two sets of standard blends. This led to the study of other possible standard fluids that would supply the hues not attained by

the two sets of blends just mentioned, and these were found in two solutions kept in every well equipped analytical laboratory—the volumetric solutions of potassium dichromate and potassium permanganate.

An investigation of these fluids showed that a one-thousandth normal permanganate volumetric solution containing 0.0313 grammes of KMnO_4 to the liter has about the same intensity of color as a one-hundredth normal dichromate solution containing 0.481 grammes of $\text{K}_2\text{Cr}_2\text{O}_7$ to the liter and blends of these two fluids are designated as to “Cro-Manganate” tints. As might be expected, these blends are extremely unstable and must be used for matching within one or two hours after mixing.

Comparing blends of these with the nitrite test mentioned above, it was found that the tint produced by a nitrite dilution representing 1 part of nitrogen in 10 million was matched by the standard “Cro-Manganate” blend 15-1 diluted to 55 per cent.

The Section then adjourned.

E. E. SMITH,
Secretary.

SECTION OF ANTHROPOLOGY AND PSYCHOLOGY

25 OCTOBER, 1915

Section met in conjunction with the American Ethnological Society, Vice-President Clark Wissler presiding.

The following programme was offered:

Marshall H. Saville, FIELD ACTIVITIES OF THE MUSEUM OF THE AMERICAN INDIAN, 1915.

Professor **Saville** outlined the operations carried on under the auspices of Mr. George G. Heye during the past year. The work achieved was both archeological and ethnological and embraced South America as well as North America. Somatological material is not to be installed by the Museum, but is turned over to the National Museum in Washington, D. C. The speaker summarized the investigations carried on by himself, Mr. Theodor de Booy and others, illustrating his lecture with slides.

The Section then adjourned.

ROBERT H. LOWIE,
Secretary.

BUSINESS MEETING

1 NOVEMBER, 1915

The Academy met at 8:15 P. M. at the American Museum of Natural History, Vice-President Charles P. Berkey presiding.

The minutes of the last business meeting were read and approved.

The following candidates for membership in the Academy, recommended by Council, were duly elected:

ACTIVE MEMBERSHIP

Lee M. Hurd, 15 East 48th Street.

ASSOCIATE MEMBERSHIP

R. S. Knappen, Columbia University.

The Acting Recording Secretary reported the following deaths:

James Geikie, Honorary Member of the Academy since 1901,

Sir David Gill, Honorary Member of the Academy since 1898.

The Academy then adjourned.

HENRY E. CRAMPTON,
Acting Recording Secretary.

SECTION OF GEOLOGY AND MINERALOGY

1 NOVEMBER, 1915

Section met at 8:20 P. M., Vice-President Charles P. Berkey presiding.

The minutes of the last meeting of the Section were read and approved.

The following programme was then offered:

W. D. Matthew,	NEW FOSSIL PROBOSCIDEA.
Ida H. Ogilvie,	FIELD OBSERVATIONS ON THE IOWAN PROBLEM.
F. K. Morris,	GEOLOGY OF THE CAMP COLUMBIA REGION.
S. H. Knight,	FIELD RESEARCHES ON THE RED BEDS OF SOUTHEASTERN WYOMING.
D. R. Semmes,	FIELD WORK IN THE SAN JUAN DISTRICT, PORTO RICO.
E. T. Hodge,	FIELD STUDIES IN THE COAMO-GUAYAMA REGION, PORTO RICO.
Chester A. Reeds,	FOSSIL COLLECTING IN PORTO RICO.

SUMMARY OF PAPERS

Dr. **Matthew** described some new fossil Proboscidea discovered by Professor Barbour of the University of Nebraska. With the aid of lantern slides, Dr. Matthew showed a number of Professor Barbour's speci-

mens and drawings, illustrating the stages of development of this interesting group.

Miss **Ogilvie** said in abstract: Only about thirty-five years ago the controversy was going on as to whether there was really an ice age. That question was hardly settled when the problem of two ice ages came to the front. One by one ice ages were added, until at the beginning of the present century we had six described and named, and naturally there were corresponding interglacial stages. The six ice ages, with their corresponding interglacial ages, have been incorporated in our text-books and seemed to be passing into tradition when in 1909 Mr. Frank Leverett raised the question as to whether one of them really existed. He did not specifically attack the Iowan age, but in a paper on the correlation of American and European glacial deposits he left it out. In the various papers which he and others have written there have been various lines of attack, and various conclusions have been reached as to what the Iowan drift is. Briefly, these were: that it is the weathered top of the Kansan; that it is contemporaneous with the Illinoian, coming from the Kewatin center at the time that the Illinoian came from the Laurentide; that it is an interglacial deposit, formed contemporaneously with the loess. The controversy was complicated by the fact that the only complete glacial maps of the region were those published by McGee in the *Eleventh Annual Report U. S. Geological Survey*, in which only two ice ages were recognized. These upper and lower drifts are in some places the sub-Aftonian and the Kansan, and in others the Kansan and the Iowan. Samuel Calvin, to whom we owe most of our knowledge of Iowa Pleistocene geology, always defended the existence of the Iowan as a separate age, his death unfortunately occurring before the question was settled.

Feeling that this question of the number of ice ages is the most important problem in glacial geology to-day, I visited the typical Iowan area. Having seen it, I feel convinced that, whatever the Iowan is or is not, it is not identical with the Kansan. The Kansan drift is blue and clayey, the Iowan yellow and powdery, but with huge granite boulders. They often occur together, with the Buchanan gravel between, and there is no question but that two drifts are there. The topography of the Iowan surface is young; it is for the most part a nearly flat plain with very gentle undulations. The Kansan (in places where it was never covered by the Iowan) is much more deeply eroded, rivers having cut through it and made gorges in the rock below. The Iowan drift is unaccountably absent from many places, and is never thick. In the various cuts and gravel pits where I saw it, it was never more than seven feet in thickness, and usually less. Its borders grade into loess, and the origin

and history of the loess add a complication to the problem. The best evidence that I saw that the Iowan was really a distinct ice-advance, and later than the Kansan, was in a cut of the interurban line that runs from Iowa City to Cedar Rapids. Here the Kansan lies below, blue and clayey and slightly weathered on top. Above this lies the Buchanan (= Sangamon) interglacial gravel. This is highly oxidized and ranges in texture from fine flour up to pebbles six or eight inches in diameter. It is roughly stratified, is partly cemented by iron oxides and is brown and black in color. This gravel and the surface of the Kansan below is thrown into a series of folds, the stratification lines following the folds. These contortions can only be explained by a thrust of some kind, and as folding in the deep-seated sense is out of the question, they must be due to pressure from ice. The Kansan also suggests having been overridden by ice, in that it has a series of prominent joint cracks dipping toward the west and suggesting pressure from that direction. On top of the folded beds lie undisturbed drift, of the yellow color characteristic of the Iowan. It is about two feet thick across the top of the folds, but toward the western end of the section the upper till and the Buchanan gravel together dip toward the west, the till thickening to about seven feet. Westward it grades into fossiliferous loess, the boundary between loess and Iowan drift being almost impossible to draw. There seems no doubt, then, that there was a glaciation in Iowa later than the Kansan; the highly weathered character of the Buchanan points to a long period of deglaciation and hence to a complete retreat of the ice at that time. The question of whether the Iowan may be contemporaneous with the Illinoian is more difficult to prove. Since the Iowan ice came from the Kewatin center and the Illinoian from the Laurentide, any comparison of material would be futile. And as Leverett has pointed out, a comparison of the stage of erosion of two places has little significance unless they are nearer than the localities in question. So this phase of the question is still unsettled.

Mr. **Semmes** said in abstract: During the summer of 1915 the New York Academy of Sciences, in connection with the Insular Government of Porto Rico, undertook a careful geological survey of a section of the island extending north-south from longitude $66^{\circ} 06'$ to $66^{\circ} 27'$, or approximately from the city of San Juan to a point about twenty miles to the west. The writer was assigned the northern half of this section, an area extending as far south as the town of Barranquitas.

On arriving in the field, a topographic map on the scale of two inches to the mile and 250' contour interval was first made, as a basis for geological observations.

The areal geology of the district was next studied. The formations were generally subdivided as follows:

Younger series:

Recent deposits—alluvium—San Juan lime sand.

Tertiary deposits—limestones and shales.

Older series:

A complex of pyroclastic tuffs, ashes and breccias grading into essentially hydroclastic sandstones, shales, conglomerates and limestones, intruded by numerous igneous masses of great variety, all of which are probably pre-Tertiary.

The areas of economic importance are:

The gold mines south of Corozal.

Auriferous quartz stringers in the older series, usually occurring in fractured tuffs.

The gold placers near Corozal.

The streams in this vicinity afford some gold and occasional particles of platinum.

The copper prospects in the barrio of Pasto.

Impregnations along crushed zones in a porphyritic intrusion.

Since returning from the field the writer has been engaged in a microscopic study of the petrogenetic relations of the various formational units and in the determination of the more important fossils collected in the Tertiary formations.

Mr. **Hodge** discussed the physiographic history of the Coamo-Guayama district located on the south central portion of Porto Rico and which recorded the following events: (1) peneplanation, (2) burial, (3) uplift and development of a consequent drainage on the limestone coastal plain which covered part of the island, (4) attempt on the part of streams to attain structural adjustment, and finally, (5) recent uplift. Because of deep residual soil, few outcrops and absence of fossils, accurate detailed stratigraphic correlation proved impossible, but in a large way the rocks have been grouped and their succession worked out. The bedded formations, aside from minor irregularities, dip 60° - 70° south and strike north 40° west throughout most of the area, excepting the southeast portion where they assume a synclinal structure. The most characteristic feature of the area consists of the hundreds of separate and distinct intrusions and extrusive rocks with their associated tuffs and breccias. These pyrogenic rocks are mostly of an andesite composition and all highly altered to carbonates, so much so that previous workers have considered many of

them limestones. In this district occur a group of thermal springs which are directly related to a great fault. It is of interest in this connection to note that, aside from those in the Tertiary limestones (which have no bearing on this problem) the only true springs in Porto Rico are thermal springs—three in number—related to fault zones.

Dr. **Reeds** said in abstract: During June and July, 1915, two members of the staff of the American Museum of Natural History—Dr. Chester A. Reeds, in charge, and Mr. Prentice B. Hill, interpreter and assistant—collected fossils in Porto Rico under the auspices of the New York Academy of Sciences and the Porto Rican Government.

The collecting was confined almost entirely to the sedimentary beds of the "older" and "younger" series defined by Professor Berkey⁴ in his report, "Geological Reconnaissance of Porto Rico." It was conducted from the following centers: Aguadilla, San Sebastian, Juana Diaz, Ponce, Yauco, San German, Arecibo and San Juan.

The most prolific localities in the "younger" series were as follows: the Collazo River and vicinity near San Sebastian; the railroad cut, west abutment of the American Railroad bridge over the Guajataca River, near Quebridillas; the shale and limestone exposures to the northwest and southwest of Juana Diaz on the Jacaguas River; on the Ponce-Penuelas road 4 km. west of Ponce; at Km. 25 and exposures in the river bank north of Guayanilla; the east wall of Guanica harbor; on the Arecibo-Utuado road at various places between Km. 66 and 72; and on the Manati-Ciales road between Km. 1-2 and at Km. 9.

Fossils were collected from the dense limestones of the "older" series of the basal complex at the following localities: from the exposures to the northwest and southeast of the Guayabal Reservoir; at and near the bridge over the Descalabrado River on the road from Juana Diaz to Coamo; between Coamo Springs and the Coamo Reservoir; at various points along the road from Ponce to Adjuntas; near Penuelas: at Km. 35 on the Yauco-Sabana Grande road; from the hill to the south of Yauco; at Ensenada and from various places 1-5 kilometers northwest of Ensenada; at San German; on the road to Lajas; at Lajas; at Parguera; on the island off the coast and from the hills back of Parguera; from La Muda; and from Trujillo Alto.

The collection when shipped from San Juan consisted of 35 boxes, weighing approximately 3100 pounds. It contains 10,000 to 12,000 specimens. About 10 per cent. are rock specimens and 90 per cent. invertebrates. Only a dozen fragmentary specimens of vertebrate fossils were found. The specimens have been unpacked at the American Mu-

⁴ Berkey, C. P.: *Annals N. Y. Acad. Sci.*, Vol. 26, pp. 1-70, pls. 1-3, 1915.

seum of Natural History and about one half washed and sorted as to classes.

The vertebrate remains have been turned over to Dr. D. W. Matthew of the American Museum of Natural History for identification and description. In a jawbone with three teeth and two vertebrae he has identified ? *Halitherium antillense* n. sp. a primitive cetacean with European affinities.

In addition to the large collection of specimens, one hundred and forty-seven excellent photographs were secured.

The Section then adjourned.

D. W. JOHNSON,
Secretary.

SECTION OF BIOLOGY

8 NOVEMBER, 1915

Section met at 8:15 P. M., Dr. F. A. Lucas presiding.

At the request of the Secretary a committee was appointed by the Chair to examine and correct the minutes of the Section for the last year, for printing in the Records of Meetings. The Chair appointed Doctors Matthew and Schulte.

The following nomination for 1916 was made and approved for transmission to the Council:

For Vice-President of the Academy and Chairman of the Section, Professor Hermann von W. Schulte, Columbia University.

Dr. William K. Gregory was elected Secretary for the year 1916.

The following programme was then offered:

Chester A. Reeds, PORTO RICAN LOCALITIES YIELDING VERTEBRATE FOSSILS.

J. A. Allen, AN EXTINCT OCTODONT FROM THE ISLAND OF PORTO RICO.

W. D. Matthew, A NEW SIRENIAN FROM THE TERTIARY OF PORTO RICO.

C. R. Eastman, REPORT OF INVESTIGATION ON PALAEOZOIC FISHES.

Dr. **Reeds** said in abstract: The better known localities in Porto Rico yielding vertebrate fossils are two in number, namely, San Sebastian and Juana Diaz. These towns are situated on opposite sides of the central basal complex, constituting the "older series" as defined by Professor Berkey⁵ in his report, "Reconnaissance of Porto Rico." Near these towns

⁵ Berkey, C. P.: *Annals N. Y. Acad. Sci.*, Vol. 26, pp. 1-70, 1915.

there are exposures of lignitic shales and white limestone of the "younger series"⁶ which rest unconformably upon the "older series" and which are of Lower or Middle Tertiary age. In each locality vertebrate fossils have been found associated with unquestioned marine invertebrates in both the basal lignitic shales and the overlying Arecibo limestone.

Professor Berkey has referred to these basal lignitic shales as a part of the Arecibo formation.⁷ It may be proved in the end that they should be so classed, but for the present it will be well to separate the shales from the limestone and use other names in referring to them. The name Collazo is here applied to the lignitic shale beds in the vicinity of San Sebastian, from the typical exposures on the Collazo River, and the term Juana Diaz to the shale beds in the vicinity of Juana Diaz, particularly the shale exposures on the Jacaguas River to the northwest, west and southwest of Juana Diaz. The term Arecibo is retained for the limestone.

The most important vertebrate find has been identified by Dr. W. D. Matthew, Curator of Vertebrate Palæontology, American Museum of Natural History, as a new species of (?) *Halitherium* (see page 439 below). It consists of a lower jaw with three molar teeth and two vertebrae of a primitive Sirenian. It was collected by Chester A. Reeds, July 1, 1915, from the Juan Diaz shale exposures on the Jacaguas River one kilometer north and one kilometer west of Juana Diaz. Other fossils, some of them Sirenian, have been collected by Señor Narciso Rabell Cabrero from the Collazo shales. They are in his private collection at San Sebastian.

The tooth of a fish belonging to the family Scombridæ (mackerels and their allies) was found in the Arecibo limestone exposures on the Jacaguas River to the southwest of Juana Diaz, locality 199.

A small, very delicate bone of an indeterminate teleost was collected from the south bank of a ravine in the Juana Diaz shales, locality 226, approximately 200 feet below the base of the Arecibo limestone, from the exposure on the Jacaguas River to the southwest of Juana Diaz.

A short distance below the road bridge over the Collazo River the tooth of a hammerhead shark, *Sphyræna prisca* Agassiz, was unearthed from the lignitic shales exposed in the bed of the Collazo River.

The tooth of *Carcharias magna* (Cope) was collected from the base of a 300-foot exposure of the Arecibo limestone in the east wall of the Guajataca River canyon at a point where a native trail crosses the river. It is on Señor Rabell's ranch about ten kilometers northeast of San Sebastian.

⁶ Ibid., pp. 11-17.

⁷ Ibid., pp. 12-17.

The fish remains have been identified by Dr. L. Hussakof, Curator of Ichthyology, American Museum of Natural History.

Dr. Allen said in abstract: During the exploration of a cave in the Jobo district, near Utuado, Porto Rico, made under the direction of Dr. Boas, several hundred mammal bones were obtained, all referable to a single species of an extinct octodont rodent. These bones are well preserved and have the character and general appearance of recent bones. They include several nearly complete skulls, a large number of mandibular rami, a pelvis and many limb bones and ribs. They represent a species about the size of *Plagiodontia* and the smaller species of *Capromys*, but it is not closely related to either of these genera, nor to any other known genus. It is especially characterized by the enamel pattern of the molariform teeth, which is strikingly different from that of any other described octodont. In size, in the general form and proportions of the skull and in the oblique insertion of the grinding teeth, it resembles *Plagiodontia*, known thus far only from the type specimen from Haiti, described by F. Cuvier in 1836 and now probably extinct.

In both *Plagiodontia* and the new form from Porto Rico, which may be known as *Isolobodon portoricensis*, the transverse axis of the molars is highly oblique to the axis of the tooth-row, the obliquity of the two axes being about 45° , instead of the two axes forming a right angle, as in *Capromys*. The molariform teeth in *Isolobodon* resemble those of *Plagiodontia* not only in manner of insertion, but in size and form and in the number of enamel folds on the outer and inner borders. They radically differ from those of *Plagiodontia* in the enamel pattern of the crowns, in which latter the cement area of each tooth consists of three transverse divisions, united and continuous, thus constituting a single sigmoid area, deeply cut by the infolding of the enamel border. In *Isolobodon* the cemented portion of the crown surface of each upper molar forms two transverse, nearly equal oval areas, each entirely encircled by its own enamel border. The enamel pattern of the lower molars differs from that of the upper molars through the deep indentation of the anterior enamel area by the infolding of the enamel border on the inner side of the front third of the tooth.

The condition of the remains of *Isolobodon* indicates its recent extinction, they having undergone no change in mineralization or even in coloration. As in the case of *Plagiodontia*, it was probably exterminated by the natives, who doubtless persistently hunted it for food, as its flesh must have been highly palatable and as it was the largest indigenous mammal of the island. It is known that this fate overtook *Plagiodontia* at about the middle of the last century, as Cuvier states that it was

sought after so carefully by the natives of Haiti for its delicate flesh that it had already become extremely rare as early as 1836. And no specimen has since reached any natural history museum. *Isolobodon* has probably been extinct for a few hundred years.

Dr. **Matthew** said in abstract: A number of specimens of fossil vertebrates were secured by Dr. Chester A. Reeds on the Natural History Survey of Porto Rico under the auspices of the New York Academy of Sciences. Among these is the lower jaw of a Sirenian associated with two vertebræ from marine Tertiary limestones of uncertain horizon. The jaw is referred to the genus *Halitherium* of the European Oligocene and Miocene and represents a new species, *H. antillense*, nearest to *H. christoli*.

Halitherium is a primitive stage of the dugong family (Halicoridae), now found only in the Indian Ocean and Red Sea, but abundant around the shores of Tertiary Europe. It has never before been reported from this side of the Atlantic. The other family of Sirenians, Manatees, occur on both sides of the Atlantic, but not in the Indian or Pacific oceans, and are now limited to the tropics. The distribution of the dugongs was therefore wider than has been supposed, extending to both sides of the Atlantic as well as to the eastern seas, where they still survive.

The anterior grinding teeth (premolars) in the dugong series are progressively reduced; in the manatees they become molariform. The molar premolar formula is briefly considered. The writer accepts Abel's view that there are but three true molars in the Sirenians and not more than four premolars. The last milk molar is retained very late and sometimes intercalated between p_4 and m_1 .

Dr. **Eastman** presented in abstract an account of the more important results of investigation of a large series of Paleozoic fish remains belonging to the American Museum, the U. S. National Museum, and other institutions, the work having been in progress for over a year.

Ordovician fish remains from a newly discovered locality in Colorado were described, and the systematic position of one of the oldest known Ostracoderms, *Astraspis* Walcott, was shown, in the light of unusually well-preserved specimens, to be representative of a distinct family allied to the Psammosteidae. The large dorso-median plate of *Astraspis* is of compound nature, being formed of fused tuberculated tesserae. A similar tessellated structure has been observed in Cephalaspids and Psammosteids, and more recently in specimens from Dorpat, Russia, described by Preobrazhensky in 1910 under the name of *Dyptychosteus tessellatus*. Another specimen in the Dorpat Museum described by the last-named author as a new species of *Psammosteus* (*P. imperfectus*) appears to be truly refer-

able to the peculiar and little-known genus *Ceraspis*, first reported by Schüter from the Eifel Devonian.

A brief consideration was made of the evidence upon which Jaekel, Dollo and others have recently advocated the view that Ptyctodonts are Arthrodire, and that the latter group, together with Ostracoderms, are derived from primitive sturgeons. Comment was made upon Jaekel's theoretical reconstruction of the so-called shoulder-girdle (in reality a totally different structure) of *Rhynchodus* and upon the disputed question of the restored dentition of Mylostomids. The typical specimen of *Dinognathus ferox* was exhibited and held to afford reliable means for homologizing the several components of the Mylostomid and Dinichthyid types of dentition. A discussion followed of recent interpretations of the dental structures grouped under the head of Edestidæ, and of the conjectural association of Cochlodont and Psephodont crushing plates in the mouth of Carboniferous sharks.

New discoveries were reported of fossilized brain structures and auditory organs in ganoid fishes from the Carboniferous, as well as the unique occurrence of otoliths in the Permian genus *Palæoniscus*. A slab was also exhibited in which were preserved complete skeletons of a probably new species of *Cœlacanthus*, discovered by Dr. E. H. Barbour in the Coal Measures of Kansas.

The Section then adjourned.

WILLIAM K. GREGORY,
Secretary.

SECTION OF ANTHROPOLOGY AND PSYCHOLOGY

22 NOVEMBER, 1915

Section met in conjunction with the New York Branch of the American Psychological Association at Columbia University, Professor H. L. Hollingworth presiding.

The following nomination for Vice-President of the Academy and Chairman of the Section was approved for transmission to the Council:

Professor J. McKeen Cattell, Columbia University.

Dr. Robert H. Lowie was elected Secretary of the Section for the year 1916.

The following scientific programme was then offered:

Charles K. Taylor, SOME RELATIONS BETWEEN MEMORY SPAN, ATTENTION, SCHOOL-GRADE AND AGE.

- T. H. Ames,** COLOR THERAPY.
H. L. Hollingworth, WHY THE LOWER SENSES ARE UNÆSTHETIC.
M. J. Van Wagenen, A PRACTICE EXPERIMENT.

SUMMARY OF PAPERS

Mr. **Taylor** said in abstract: A series of experiments were made with about 500 children in the four upper grades of a public school, as a result of which interesting relations seemed to appear between memory-span, attention, school-grade and age.

Groups of numbers, varying from three to twelve digits, were dictated to the children, who wrote from memory each number as soon as it was dictated. While this was going on the class-room was made as quiet as possible and free from disturbing elements. Two series of numbers, ten numbers to the series, were given under these conditions. Not more than two or three children, it was found, could remember and write down a number of twelve digits after dictation, a few more remembered eleven, more remembered ten, and so on.

It was found, first, that the average numbers remembered by the different grades were larger as the grades advanced in age. It was also found that of children of the same age in different grades, those in the lower grades could not remember as large numbers as those in higher grades. Also there was a close correspondence between the memory average of the children and their averages given in the monthly reports.

After a period of rest, two more series of numbers were dictated, similar to the first two; but this was done while the teacher read aloud from an interesting book, thus making a disturbing element. By comparing averages in the two sets of series one could gain an idea as to the attentive powers of the children.

It was found that though there was some relation between the school-report and "attention" and the school-grade and "attention," that the most marked relation seemed to be between age and attention. For instance, all of the sixteen-year children did as well with the disturbing element or better than with the quiet. Only 42 per cent. of the fourteen-year children and 32 per cent. of the twelve-year children did as well or better with the disturbing element as they did without it. With the children of eleven and under all made poorer averages with the disturbing element than without it.

Dr. **Ames** said in abstract: References brought together, ranging from the most ancient superstitions and folklore to modern material from psychological laboratories, give evidence that color was used to conciliate or

ward off supernatural beings, to ameliorate abnormal physical and mental conditions and to change the emotional states of normal people.

Color acts for these ends in various ways: By magical charms or sorcery, as a scape-goat, by thinking processes, or by homeopathic and allopathic procedure.

Not only are masses and individuals affected in a similar manner by color, but also the masses and individuals of all nations and all times. The experiment by Wells in the *Psychological Bulletin* of 1910, stating that colors at the red end of the spectrum are stimulating, that those in the central part are tranquilizing and those at the purple end subduing agrees in its results with those to be obtained from a study of ancient superstitions.

While the uses of color never have been and may never be demonstrated to be of such value as to become commercialized, still there is sufficient evidence to warrant us in believing that, apart from any purely utilitarian or purely æsthetic use, color has a place in therapeutics.

Professor **Hollingworth** reviewed the various reasons that have been suggested in explanation of the unæsthetic value of the lower senses. Such factors as abundance, ecclesiastic censorship, number of qualities, sharpness of discrimination, reaction time, inertia and life-span, spatial characteristics, immediate affective value, materiality, consumption of stimulus, utilitarian function, ontogenetic and philogenetic development, vividness of imagery, organization and systematic relations within the modality, social character, range of stimulus, perceptual value, tendency to adaption, etc., were considered. Criticisms were offered of the theory that "the function of art is to please" and the intellectual character or "meaning" function of æsthetic manipulation was emphasized.

Mr. **Van Wagenen** said in abstract: Table I gives the Pearson coefficients between the work done at various parts of two practice periods and a final test period. The material consisted of a set of ten paired associates, the stimuli being the first ten letters of the alphabet arranged in chance order, the associates being the next ten letters, also arranged in chance order. The subjects were forty university students in a class in elementary psychology, who practised two periods of thirty-two minutes each, forty-seven hours apart, and for three minutes forty-seven hours later.

The three-minute test was followed by another practice period on a new set of paired associates, the stimuli consisting of the original first ten letters arranged in a new chance order, the associates consisting of the

digits 0 to 9, also arranged in chance order. The results are given in table II.

TABLE I

Minutes	Period	Minutes	Period	r
4-8	First	26-30	First	.780
4-8	First	33-37	Second	.698
4-8	First	58-62	Second	.515
26-30	First	58-62	Second	.820
26-30	First	65-67	Test (third)	.880*

*Only thirty-five subjects were present for this test. The method of rank differences was used in finding this coefficient, while the product-moments method was used in finding the other coefficients.

TABLE II

Minutes	Period	Associates	Minutes	Period	Associates	r
4-8	First	Letter-digit	4-8	First	Letter-letter	.615 ⁸
4-8	First	Letter-digit	65-67	Third	Letter-letter	.531 ⁹

A second experiment was carried out with a group of thirty-four summer-session university students, in which the same letter-letter associates were used as in the previous experiment, and in which the quantity of work done instead of the time was kept constant. During the first practice period 120 associations were made with each pair. Four weeks later 80 more associations were made with each pair. Just before the second practice period the amount that could be recalled during 200 seconds was measured, the amount being the number of correct associates that were recalled when the stimulus letters were read in varied order two seconds apart. The results are given in tables III and IV.

TABLE III

Minutes	Period	Minutes	Period	r
4-8	First	26-30	First	.727*
4-8	First	Last five	First	.753
4-8	First	4-8	Second	.541
4-8	First	Last five	Second	.604
Last five	First	Last five	Second	.845

*Probably too low, as the last five minutes were used in two cases where the work was finished during the 27th minute.

⁸ Thirty-seven subjects.

⁹ Thirty-four subjects.

TABLE IV

Amount recalled	Shortness of first practice period	r- .186
Amount recalled	Amount done during minutes 4-8	.231
Amount recalled	Rate of work during last five minutes of first practice period	.355
Amount recalled	Rate of work during last five minutes of second practice period	.538

The Section then adjourned.

ROBERT H. LOWIE,
Secretary.

BUSINESS MEETING

6 DECEMBER, 1915

The Academy met at 8:15 P. M. at the American Museum of Natural History, Vice-President Charles P. Berkey presiding.

The minutes of the last meeting were read and approved.

The following candidate for Active membership in the Academy, recommended by Council, was duly elected:

Isaiah Bowman, American Geographical Society.

The Secretary reported the death of Theodor Boveri, Honorary Member since 1910, on 16 October, 1915, and stated that the Council at its meeting on 6 December had requested Professor Edmund B. Wilson to form a suitable minute to be spread on the records of the Council.

The Academy then adjourned.

HENRY E. CRAMPTON,
Acting Recording Secretary.

SECTION OF GEOLOGY AND MINERALOGY

6 DECEMBER, 1915

Section met at 8:20 P. M., Professor J. E. Woodman presiding.

The minutes of the last meeting of the Section were read and approved.

The following programme was then offered:

- J. E. Woodman,** METALLURGICAL LIMESTONES OF NOVA SCOTIA.
A. K. Lobeck, POSITION OF THE NEW ENGLAND PENEPLAIN IN THE WHITE MOUNTAIN REGION.
Chester A. Reeds, THE J. M. ROSALES'S COLLECTION OF MESOZOIC FOSSILS FROM THE EASTERN RANGE OF THE COLOMBIAN ANDES.

**George H. Girty, NEW GENERA AND SPECIES OF CARBONIFEROUS
FOSSILS FROM THE UPPER MISSISSIPPI VALLEY.
(Read by title.)**

SUMMARY OF PAPERS

Professor **Woodman**, with the aid of maps, discussed the distribution of the metallurgical limestones of Nova Scotia and their geological occurrence. It was shown that limestones of metallurgical value are restricted to the pre-Cambrian and the Mississippian, the beds of former age, known locally as the George River Series, occurring in great abundance in central and northern Cape Breton Island, in the vicinity of St. Johns, New Brunswick, and near New Campbellton, in Nova Scotia. The metallurgical limestones of Mississippian age, known as the Windsor Series, are found both in Cape Breton and on the mainland. As these beds are non-resistant, they are usually found outcropping in lowlands eroded below the level of the Cretaceous peneplain; whereas the George River limestones withstand erosion so well that they ordinarily appear as parts of the upland surface. The composition of the limestones was described and typical specimens were exhibited.

Mr. **Lobeck** said in abstract: Three possibilities present themselves. The New England upland may be represented near the summits of the White Mountains, near their base, or somewhere in between. An unqualified choice is made and it is concluded that the upland strikes squarely and abruptly at the base of the mountains. Two types of evidence lead to this conclusion.

Field study shows that it is possible to trace the upland from its well recognized position at the base of Mount Monadnock, where it stands at an elevation of about 1100 feet, northeast along Contoocock River to near Concord, where it stands 800 feet. North of this point it rises again to about 1000 feet near Lake Winnepesaukee. In central and eastern New Hampshire it is post-maturely dissected and the broad lowlands are occupied by lakes and alluvial plains which lie 400 or 500 feet below the peneplain level. In the Lake Winnepesaukee region it is, as a matter of fact, difficult to trace the upland for the reason that it is preserved only as fragments and the region is complicated by the presence of such residuals as the Ossipee Mountains, which rise directly from the lower lake-strewn plain. However, at the base of the White Mountains, north of Lake Winnepesaukee, the upland is undoubtedly represented by a pronounced terrace-like shelf and adjacent remnants which stand at an elevation of approximately 1100 feet.

A study of maps leads decisively to the same conclusion. This is best shown by means of what are here called "projected sections." Belts of country two or three miles wide are projected upon profiles in such a way that any given point on the profile always represents the highest point in the belt opposite to such point in the profile. Such a section gives an impression strikingly similar to that which would be obtained by looking at the country itself. Projections of this kind carried from the White Mountains to the ocean across either the topographic quadrangles of western Maine or Hitchcock's map of New Hampshire represent the New England upland abutting squarely against the mountains at an elevation of a little over 1000 feet.

Results of this kind make it difficult to believe that the flat-topped spurs or "lawns" near the top of Mt. Washington and standing some 5000 feet above sea level can be considered as remnants of the New England upland, as Professor Goldthwait has suggested in the *American Journal of Science* for May, 1914. It was the interest derived from this article which encouraged a further study of the region.

The paper was discussed and favorably criticised by Mr. P. M. Foshay and Professors J. E. Woodman, C. P. Berkey and D. W. Johnson.

Dr. Reeds exhibited the Rosales's collection of fossils and discussed the geographical features of northwestern South America, the climatic zones determined by variations in elevation and the trend of the principal mountain axes. Four colored geological maps of the region were discussed, as well as typical cross-sections showing the geological structure.

Señor Rosales, the donor of the collection of fossils, was present and explained to the Academy the geological location of the points from which the fossils were collected.

The Section then adjourned.

D. W. JOHNSON,
Secretary.

SECTION OF BIOLOGY

13 DECEMBER, 1915

Section met in conjunction with the Linnean Society at 8:15 P. M., Dr. Jonathan Dwight presiding.

By request of the Secretary, the reading of minutes was dispensed with. The following scientific programme was then offered:

F. M. Chapman, THE ORIGIN OF ZONAL FAUNAS IN THE ANDES.

C. W. Beebe, A TETRAPTERYX STAGE IN THE EVOLUTION OF BIRDS.

W. K. Gregory, PRESENT STATUS OF THE PROBLEM OF THE ORIGIN OF BIRDS.

T. Barbour, SOME REMARKS UPON MATTHEW'S "CLIMATE AND EVOLUTION." (Presented by Dr. W. D. Matthew.)

Dr. **Chapman** described the American Museum expeditions to the Andes, which had been in progress for several years. He described the avian zonal faunas of the Western, Central and Eastern Andes and of the high plateaux and valleys between them and their relations to forested and arid regions. He endeavored to picture the effects of the gradual uplift of the Andean region upon the original avi-fauna, and showed how this uplift had opened new lines of extension and migration to certain north temperate and south temperate bird types.

Dr. Chapman's paper was discussed by Dr. Matthew and Mr. Murphy.

Mr. **Beebe** said in abstract: The evolution from the wing of *Archæopteryx* to that of the modern bird is comparatively simple. But the transition of the first lizard which, iguana-like, hurled its flattened, stretched body through the air, to an excellently winged creature like *Archæopteryx* has not been explained. The more evident feather zones of *Archæopteryx*—the wings and tail—would not account for success in the early stages of scaling, as there would be no adequate support for the hinder portion of the body, such as exists in the pelvic and lateral membranes of flying squirrels and lemurs and in the pelvic fins of flying fishes.

A four-day-old squab of a white-winged dove in the scanty down plumage typical of these birds showed three distinct zones of contour feathers, those of the wings and tail, and a line of twelve flight-like quills across the outer leg and femoral membrane, there being in addition six well-developed coverts above the most exposed flights. This was found to be a character common to all domestic pigeons, as well as to jacanas and owls. The lateness of the season prohibited observation on the nestlings of other birds.

It is supposed that this unexpected development of pelvic feathers is an atavistic reminder of the time when creatures living prior to *Archæopteryx* were able to scale easily through the air supported by a biplane of feather growth. This tetrapteryx stage finds support in the Berlin specimen of *Archæopteryx*, which shows distinct traces of large feathers near the base of the tail and above the tarsal feathering.

Mr. Beebe's paper was discussed by Dr. Lucas and Dr. Gregory.

Dr. **Gregory** said in abstract: Two opposing views regarding the origin of flight in birds have been developed, mostly since 1900. According to the first, advocated by Pycraft, Abel, Beebe and others, the primi-

tive birds were arboreal reptiles with long scale-covered arms, and they learned to fly after they had gone through a flying-squirrel-like stage, in which the skin and scales acted as a passive patagium and flight was learned by skimming downward to the ground. The opposing view, advocated by Nopcea and supported by Watson and Williston, was that flight began from the ground upward, the primitive types being small bipedal dinosaur-like reptiles which beat the air with their long scaly forearms as they ran along the ground. Dr. Broom's view was that the primitive birds were nearly related to the common ancestors of the dinosaurs and pterosaurs and were related to the aëtosauroids. That first they hopped on the ground, and then hopped in the trees, after the fashion of a tree kangaroo, before learning to skim down from the trees.

The speaker had made comparisons of the skulls and skeletons of all the principal types of reptiles and ancient types of birds and felt that there was strong evidence for the view advocated by Abel, Broom and others that the dinosaurs, pterosaurs, aëtosauroids and birds were divergent derivatives of small "diapsid" reptiles most nearly allied to the aëtosauroids (*Pseudosuchia*). To him the evidence indicated that the pro-aves were small arboreal quadrupedal reptiles, excellent climbers and of great activity in the trees, leaping from branch to branch like lemurs and early acquiring a grasping hallux and consolidated metatarsus. Hands much elongate, as in such agile Primates as the gibbons, digits of the manus (which in the terrestrial stage had already been reduced in number from five to three, as in certain dinosaurs) elongate, provided with sharp claws (used in climbing) and covered on the back with long scales. In short, the speaker supported the conservative view that birds had arisen in somewhat the same way as had pterosaurs and bats, namely, from very active arboreal animals, and he felicitated Mr. Beebe upon adding new and striking evidence for this view. He referred to the fact that birds and mammals had originated at about the same period in the earth's history, namely, during the arid Triassic period, and that the most distinctive characteristics of both mammals and birds were associated with the maintenance of a high and relatively stable body temperature. He thought that the acquirement of feathers, and subsequently of the power of flight, was at first a biproduct of the adaptations in the circulatory system for raising the temperature of the body and in the integument for retaining the heat.

Dr. **Matthew** outlined the arguments which had been directed by Professor Thomas Barbour against certain features of his paper on Climate and Evolution, especially those relating to the former land connec-

tions of the West Indies and to the hypothesis of the accidental transportation of animals to islands by "natural rafts."

The Section then adjourned.

WILLIAM K. GREGORY,
Secretary.

ANNUAL MEETING

20 DECEMBER, 1915

The Academy met in Annual Meeting on Monday, 20 December, 1915, at the Hotel Manhattan, at the close of the Annual Dinner, President George F. Kunz presiding.

The minutes of the last Annual Meeting, 21 December, 1914, were read and approved.

Reports were presented by the Corresponding Secretary, the Recording Secretary, the Librarian and the Editor, all of which were received and ordered placed on file.

The Treasurer's report showed a net cash balance of \$488.17 on hand at the close of business 30 November, 1915. On motion, this report was received and referred to the Finance Committee for auditing.

A report of the Committee on Extension (Porto Rico Committee) was read by the Chairman, Professor N. L. Britton. It was voted that this report be received and placed on file.

It was also voted that the Academy record its thanks to the committee for its able conduct of the Survey.

The following members of the Academy were elected Fellows, the Secretary being authorized to cast a single affirmative ballot for the list as presented:

L. A. Adams, Columbia University,
Isaiah Bowman, American Geographical Society,
R. L. Ditmars, New York Zoölogical Park,
G. Clyde Fisher, American Museum of Natural History,
A. J. Goldfarb, College of the City of New York,
Victor E. Levine, College of Physicians and Surgeons,
H. J. Muller, Rice Institute, Houston, Texas.

The Academy then proceeded to the election of officers for 1916. The ballots prepared by the Council in accordance with the By-Laws were distributed. On motion, the Secretary was authorized to cast a single affirmative ballot for the list of nominees as presented.

President: MICHAEL IDVORSKY PUPIN.

Vice-Presidents: ERNEST E. SMITH (Section of Astronomy, Physics and Chemistry), J. McKEEN CATTELL (Section of Anthropology and Psychology), DOUGLAS W. JOHNSON (Section of Geology and Mineralogy), H. VON W. SCHULTE (Section of Biology).

Corresponding Secretary: HENRY E. CRAMPTON.

Recording Secretary: EDMUND OTIS HOVEY.

Treasurer: HENRY J. COCHRAN.

Librarian: RALPH W. TOWER.

Editor: EDMUND OTIS HOVEY.

Councilors (to serve three years): CHARLES P. BERKEY and CLARK WISSLER.

Finance Committee: FREDERICK S. LEE, JOHN TATLOCK and W. J. MATHESON.

At the close of the elections the retiring President, Dr. **George F. Kunz**, delivered an address, entitled "Precious Stone Minerals: their Archæology and Mineralogy."

Through the courtesy of the telephone company, an interesting trans-continental telephonic programme followed. This began with a series of motion pictures showing scenes along the route of the transcontinental line with a descriptive explanation by Mr. W. F. Schmidt. Mr. H. W. Casler, Division Advertising Manager of the New York Telephone Company, then assumed charge of the line, and after the transcontinental roll call from New York to San Francisco, officers, members and guests of the Academy conversed with representatives of the California Academy of Sciences. The New York representatives were: President Kunz, President-elect Pupin, Professor N. L. Britton, Mrs. N. L. Britton, Professor Charles P. Berkey, Professor Henry Fairfield Osborn, Dean Frederick A. Goetze, Professor Charles Baskerville, Mr. H. T. Dickinson, Mrs. H. T. Dickinson, Mr. Henry J. Cochran, Professor Bashford Dean, Mrs. C. P. Berkey, Professor H. E. Crampton and Mr. A. A. Anderson. The California representatives were: Professor C. E. Grunsky, Mr. William H. Crocker, Professor Percival Lewis, Miss Alice Eastwood, Professor Bailey Willis, Dr. Roy E. Dickerson, Dr. Frank T. Green, Mrs. Zeia Nuttall and Dr. Barton W. Evermann.

The programme also included music played at San Francisco and the sound of the Atlantic waves in connection with a series of motion pictures showing the surf at Cliff House and Seal Rocks.

It was voted that the thanks of the Academy be tendered to Mr. Casler, Mr. Schmidt and their associates for their kindness and courtesy in preparing and conducting the notable demonstration.

A series of motion pictures on "Diamond Mines in South Africa" was presented with an explanatory talk by Mr. **H. T. Dickinson**, General Manager of the De Beers Company at Kimberley.

On motion, the Academy presented its thanks to Mr. Dickinson for his address.

The Academy then adjourned.

HENRY E. CRAMPTON,
Acting Recording Secretary.

REPORT OF THE CORRESPONDING SECRETARY

We have lost by death during the past year the following Honorary Members:

Authur Auwers, elected 1898, died 24 January, 1915,
Theodor Boveri, elected 1910, died 16 October, 1915,
James Geikie, elected 1910, died 2 March, 1915,
Sir David Gill, elected 1898, died ———,
Ambrosius A. W. Hubrecht, elected 1896, died 22 March, 1915.

and three Corresponding Members:

Orville A. Derby, elected 1890, died 27 November, 1915,
Theodore B. Comstock, elected 1877, died 26 July, 1915,
Arthur Williams Wright, elected 1876, died 19 December, 1915.

There are at present upon our rolls 42 Honorary Members and 112 Corresponding Members.

Respectfully submitted,

HENRY E. CRAMPTON,
Corresponding Secretary.

REPORT OF THE RECORDING SECRETARY

During the year 1915 the Academy held 11 business meetings and 25 sectional meetings, at which 67 stated papers were presented, as follows:

Section of Geology and Mineralogy, 26 papers; Section of Biology, 16 papers; Section of Astronomy, Physics and Chemistry, 5 papers; Section of Anthropology and Psychology, 20 papers.

Three of the sectional meetings were of general character and of particular interest and were followed by a social hour, with refreshments, in one of the exhibition halls of the Museum.

The first was held under the auspices of the Section of Biology on the evening of 11 January, when Professor J. C. Bose of Presidency College,

Calcutta, India, lectured upon "Plant Autographs and their Revelations." The second was held on 22 March, under the auspices of the Section of Anthropology and Psychology, when Professor Raymond Dodge delivered a lecture, entitled "Incidence of the Effect of Moderate Doses of Alcohol on the Nervous System." The third, under the auspices of the Section of Astronomy, Physics and Chemistry, was delivered on 26 April, and consisted of a lecture by Dr. Arthur L. Day upon "The Volcano Kilauea in Action."

At the present time the membership of the Academy is 491, which includes 472¹ Active Members (of whom 22 are Associate Members, 125² Fellows, 99 Life Members and 11 Patrons) and 19 Non-resident Members. There have been 11 deaths during the year, 17 resignations have become effective and eight names have been dropped from the roll. Twenty-nine new members have been elected during the year and one former member has been restored to Active Membership and seven have commuted their annual dues by a single payment of \$100 each. One name has been transferred to the Life Membership list on account of twenty-five years' payment of annual dues. One Associate Member has taken up Active Membership and one Active Member has been temporarily transferred to Associate Membership. As the membership of the Academy a year ago was 497, there has been a net loss of six during the year 1915. Record is made with regret of the loss by death of the following Active and Associate Members:

Mrs. P. H. Barhydt, Active Member since 1907,
R. A. Canfield, Active Member since 1905,
Miss Grace H. Dodge, Active Member since 1907,
Mrs. M. A. P. Draper, Active Member since 1898,
James C. Fargo, Active Member since 1878,
Thomas Hubbard, Active Member since 1905,
Frank Hustace, Active Member since 1907,
John E. Parsons, Active Member since 1896,
Albert Plaut, Active Member since 1910,
Samuel Thorne, Active Member since 1899,
Charles T. Wills, Active Member since 1897.

Respectfully submitted,

HENRY E. CRAMPTON,
Acting Recording Secretary.

¹ Including one member elect who has not yet paid his first annual dues.

² To this number must be added the seven Fellows elected at the Annual Meeting, 20 December, 1915.

REPORT OF THE LIBRARIAN

The New York Academy of Sciences has received during the current year by gift and exchange only one hundred one volumes and some two hundred fifty numbers, representing about one half of the normal accessions. Because of the insecurity of transportation, practically none of the learned societies in Russia, Germany, Austria, Italy and the Balkan States are dispatching their publications.

The Library of the New York Academy of Sciences finds an increased usefulness each year, with an appreciation on the part of the scientists for the admirable collection which it possesses.

Respectfully submitted,

R. W. TOWER,
Librarian.

REPORT OF THE EDITOR

The parts of the Annals which have been published this year are the following:

VOLUME XXIV

	Pages
W. D. Matthew—Climate and Evolution.....	171–318
H. von W. Schulte and F. Tilney—Development of the Neuraxis in the Domestic Cat to the Stage of Twenty-one Somites.....	319–346
E. O. Hovey—Records of Meetings of the Academy.....	347–406
Charter and Organization of the Academy.....	407–412
Constitution and By-laws.....	413–420
Membership of the Academy.....	421–432
Index.....	433–443

VOLUME XXVI

C. P. Berkey—Geological Reconnaissance of Porto Rico.....	1–70
F. E. Lutz—List of Greater Antillean Spiders, with Notes on their Dis- tribution.....	71–148
Henryk Arctowski—Volcanic Dust Veils and Climatic Variations.....	149–174
C. C. Mook—Statistical Study of Variation in <i>Spirifer mucronatus</i> ...	175–214
H. F. Osborn—Review of the Pleistocene of Europe, Asia and North- ern Africa.....	215–315
W. K. Gregory—Present Status of the Problem of the Origin of the Tetrapoda, with Special Reference to the Skull and paired Limbs.....	317–383
V. E. Levine—Biochemical Studies of Selenium.....	385–394

There is likewise in press a paper by T. Barbour entitled "Some Remarks upon Matthew's 'Climate and Evolution,'" with supplementary

note by W. D. Matthew. The publication Committee has accepted a paper by J. A. Allen entitled "An Extinct Octodont from the Island of Porto Rico, West Indies," and one by W. D. Matthew entitled "A New Sirenian from the Tertiary of Porto Rico, West Indies," for publication in Volume XXVII of the Annals.

Respectfully submitted,

HENRY E. CRAMPTON,
Acting Editor.

REPORT OF THE TREASURER

MEMBERSHIP

Paid up, Active Members (4 of these were elected after 1 May and paid \$5 for 1915).....	304
Paid up, Associate Members.....	18
Delinquent Active and Associate Members.....	44
Life Members and Patrons.....	110
	<hr/>
	476 ¹

RECEIPTS

DECEMBER 1, 1914—NOVEMBER 30, 1915

Cash on hand, December 1, 1914.....	\$1,274.97
Life membership fees.....	700.00
Patronship fee.....	1,000.00

Income from investments:

Interest on mortgages on New York City real estate..	\$1,002.54
Interest on railroad and other bonds.....	1,375.00
	<hr/>
	2,377.54
Interest on bank balances.....	34.42
Active membership dues, 1909.....	\$10.00
“ “ “ 1910.....	10.00
“ “ “ 1911.....	10.00
“ “ “ 1912.....	30.00
“ “ “ 1913.....	60.00
“ “ “ 1914.....	265.00
“ “ “ 1915.....	3,020.00
“ “ “ 1916.....	15.00
	<hr/>
	3,420.00
Associate membership dues, 1914.....	6.00
“ “ “ 1915.....	54.00
“ “ “ 1916.....	3.00
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	63.00

¹ Including four deceased members whose dues have been paid to the end of the year.

RECORDS OF MEETINGS

455

Sale of publications.....	405.22
Subscriptions to annual dinner (1914).....	205.00
Exchange on Grand Rapids bonds.....	30.00
Porto Rico Survey (subscriptions).....	1,500.00
Porto Rico Government (refund of advances made on account of field expenses).....	2,061.49
Cash on note in bank.....	2,000.00
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Total.....	\$15,071.64

DISBURSEMENTS

DECEMBER 1, 1914—30 NOVEMBER, 1915

Publications on account of Annals.....	\$3,474.05
Publication of <i>Bulletin</i>	577.00
Recording Secretary's expenses.....	298.91
Recording Secretary's and Editor's allowances.....	1,500.00
Esther Herrman Research Fund (grants).....	250.00
John Strong Newberry Fund (grants).....	100.00
General expenses.....	147.95
General meetings.....	730.85
Annual meeting and dinner (1914).....	255.13
Porto Rico Survey (advances for field expenses).....	4,999.63
Section of Geology and Mineralogy.....	25.00
Section of Biology.....	13.90
Section of Astronomy, Physics and Chemistry.....	14.02
Section of Anthropology and Psychology.....	25.00
Special Membership Committee.....	125.70
Payment of note in bank.....	2,000.00
Interest on note in bank.....	46.33
Cash on hand.....	488.17
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Total.....	\$15,071.64

BALANCE SHEET, 30 NOVEMBER, 1915

Investments (cost).....	\$42,332.92	Permanent Fund	\$23,574.20
Cash on hand.....	488.17	Publication Fund	3,000.00
		Audubon Fund	2,500.00
		Esther Herrman Research Fund	10,000.00
		John Strong Newberry Fund	1,000.00
		Income Audubon Fund....	745.83
		Income Esther Herrman Fund	1,762.27
		Income Newberry Fund....	238.79
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\$42,821.09		\$42,821.09	

PROPERTY

		<i>Cost</i>
Lampe Mortgage.....	at 5 per cent..	\$12,000.00
Deane-Brennan Mortgage.....	at 5½ per cent..	4,036.67
4 Detroit City Gas Company's bonds.....	at 5 per cent..	4,000.00
3 Grand Rapids Gas Light Company's bonds.....	at 5 per cent..	2,880.00
10 Madison Gas and Electric Company's bonds....	at 6 per cent..	10,400.00
1 Binghamton Gas and Electric Company's bond..	at 5 per cent..	995.00
1 Quebec-Jacques Cartier Electric Co.'s bond....	at 5 per cent..	965.00
1 San Antonio Gas and Electric Company's bond..	at 5 per cent..	487.50
1 San Antonio Traction Company's bond.....	at 5 per cent..	487.50
5 U. S. Steel Corporation bonds.....	at 5 per cent..	5,081.25
Participation bond of Lawyers' Mortgage Co.....	at 5 per cent..	1,000.00
		<hr/>
		\$42,332.92

HENRY J. COCHRAN,
Treasurer.

10 MARCH, 1915.

Examined and found to be correct.

BASHFORD DEAN,

JOHN TATLOCK,

Auditing Committee.

REPORT OF THE PORTO RICO COMMITTEE

A scientific survey of Porto Rico was inaugurated by the Council of the Academy at its regular meeting in November, 1913, upon a report of a committee previously appointed to recommend a plan for investigation, made possible by an offer of Mr. Emerson McMillin, at that time President of the Academy, to contribute \$1,000 a year for a period of five years, and an appropriation of \$500 a year by the Council from Academy's funds for a similar period, and by coöperation offered by the American Museum of Natural History, the New York Botanical Garden, scientific departments of Columbia University and New York University, and other institutions. The Insular Government of Porto Rico included an item of \$5,000 for the survey in its budget for 1914-15 and again in the budget for 1915-16, and it has been requested to continue this subsidy for three years longer.

The Committee of the Council charged with the direction of the survey consists of Professors Britton, Crampton, Kemp, Boas and Poor. The preliminary reconnaissances were made by Professors Britton and Crampton during the winter and early spring of 1914, and the work has since progressed continuously, in the field and in the laboratory. The Committee has secured the aid and advice of a large number of specialists in various fields.

Collections of geological, paleontological, botanical, zoölogical and archæological specimens, aggregating many thousands, have already been brought together, and, after being studied, are being divided among the coöperating institutions, and sets of duplicates are being returned to Porto Rico to form a natural history museum there.

It is the opinion of the committee that the further prosecution of this investigation and the publication of its results, which are planned to occupy a series of volumes of the Academy's Annals, will make Porto Rico the key to geological and biological knowledge of the West Indies.

The committee submits, by subject, the following account of the progress of the work during the past year:

1. GEOLOGY

BY PROFESSOR CHARLES P. BERKEY, ACTING FOR PROFESSOR KEMP

Early in the year a report of the first reconnaissance geological expedition was published. This has been distributed by the New York Academy and a certain number of copies have been sent to Porto Rico for general distribution. The report was written by Dr. Berkey, and undertook to give a general statement of the geological structure and make-up of the island. The report is available for additional distribution.

During the season of 1915 three special parties were sent to Porto Rico to carry on geological investigations. One of these was organized to continue general reconnaissance work and to determine certain definite stratigraphic questions connected with the Tertiary deposits. The other two were given special areas to map and study in detail. In addition to these undertakings, a special investigation was made of the supposed oil shales of the island, in compliance with special request. The division of the work is indicated as follows:

Dr. Chester A. Reeds, accompanied by Mr. Prentice B. Hill, spent the months of June and July in Porto Rico, studying the sedimentary beds on the western portion of the island, both on the north and on the south sides. The special object in view was to determine the exact age of the succession of beds represented in the "younger" series and collect such material as might be necessary for the subdivision of this series, if such an undertaking seemed to be possible; and, in addition, to collect material for its special paleontological interest. A collection of about 3,000 pounds, consisting of over 10,000 specimens, was made, and a considerable number of forms of special interest have already been noted. On account of the large amount of material and the difficulty of organizing

it, the actual bearing on the problem of stratigraphy that was set for this party is not yet ready for statement.

Mr. Edwin T. Hodge was given the special problem of determining the possible value of the oil shales in Porto Rico. Three weeks in June were spent in this investigation, collecting material and making the appropriate tests. Samples were obtained from 25 different localities, representing the most promising known occurrences in the island. All of these were investigated for oil content. The results in all cases were negative with the exception of three specimens, which showed simply traces. One of these specimens came from a shale midway between Adjuntas and Lares. Another came from a road between Las Vegas and Mayaguez, between kilometer post 11 and post 15. The third came from the farm of Signor Policarpo Domeneck, near San Sebastian. As a result of the investigation, it is concluded that there is not sufficient evidence of petroleum content to encourage investment or exploitation.

Mr. Hodge spent the rest of the season, July, August and September, in mapping and making a detailed, structural study of the Coamo region. This is a district reaching from the vicinity of Guayama on the east to the Descalabrado River on the west, and inland to Barranquitas. A topographic base map was made and the geology was covered for this area and is being put into condition for publication. It is intended as a detailed study, and, being approximately midway on the south side of the island, is intended to serve as a standard geological study for adjacent districts.

In addition to the general geological matters, a special study has been made by Mr. Hodge of the thermal springs of the island, based especially on a detailed study of the Coamo spring, and others in the immediate district. Mr. Hodge's results on all these lines will be available for publication before the next field season.

Mr. D. R. Semmes was given a district on the north side of the island, immediately opposite the section covered by Mr. Hodge. It extends from San Juan on the east to and beyond Corozal on the west, and inland to the vicinity of Barranquitas to join with the work of Mr. Hodge. This study is intended to serve as a standard investigation of the north side of the island and to make, in connection with that of Mr. Hodge, a complete, detailed cross-section of the whole island. The same methods of work were followed by Mr. Semmes as were employed on the other districts, so that a more accurate base map has been prepared and the geology has been determined. It is expected that the result of this study will be available for publication before the time of the next field season.

2. ZÖOLOGY

BY PROFESSOR HENRY E. CRAMPTON

Professor H. E. Crampton's field-work included part of January, 1915. During his sojourn renewed studies of land organisms were made in the Aibonito-Coamo section, while in addition the general reconnaissance of the island was extended so as to include the Quebradillas-Isabella area and the southwest region centering about Guanica. Among the novel items discovered in the northwest are fresh-water sponges and specimens of the peculiarly interesting crustacean *Brachippus*.

Dr. F. E. Lutz and Mr. A. J. Mutchler were in the field from May until July 12, and from various parts of the island they obtained about 15,000 insects of all orders and an additional series of spiders. This mass of material has been mounted, labeled, and assorted into the larger groups. Dr. Lutz has devoted much time to the detailed study of the bees among the Hymenoptera, and Mr. Viereck has been engaged temporarily by the Museum to investigate the parasitic Hymenoptera. Some new species and many new records have been established. Messrs. Leng and Mutchler have made substantial progress in the study of the Coleoptera, and Mr. Frank E. Watson has continued the investigations of the Lepidoptera.

Mr. R. W. Miner and Mr. H. Mueller spent several weeks in the Guanica region, and collected extensively in the harbor itself, and on the coast and reefs to the east and to the west. In all cases particular attention was paid to the environmental situations from which the specimens were taken. Additional studies were made in Condado Bay and in certain characteristic land-regions. About 8,000 marine specimens were collected by this party; they have been assorted into their phyla and systematic work has been prosecuted in certain divisions.

Professor Raymond C. Osburn also completed, in July, his studies in the deeper water organisms, which were carried on in the Guanica region especially. About 2,000 specimens were taken by dredging in various depths from the shallows near the shore to the 100-fathom line. Professor Osburn will work up the Bryozoa, in which he is interested as a specialist.

A paper by Dr. F. E. Lutz on the distribution of Arachnida has clearly demonstrated the value of the Porto Rico collections for fundamental studies in zoölogy. Briefer notes on certain species of fishes have been published by Mr. J. T. Nichols, who participated in the field work of last year. Other articles of a general nature are in course of preparation.

3. ARCHÆOLOGY

BY PROFESSOR FRANZ BOAS

During the past year three distinct lines of anthropological work have been taken up: (1) an investigation of the physical characteristics of the Porto Ricans, (2) an inquiry into their folklore, (3) researches on the antiquities of the island.

The first of these inquiries had for its object the study of conditions of growth of the body in a tropical environment. It is generally assumed that heat has the effect of accelerating the physiological development, so that in warm climates children reach maturity earlier than in temperate zones. Our inquiries do not substantiate this view. The material has not yet been collated; but from the general character of the data, I venture to say that they will be of the very greatest importance for practical measures relating to the hygiene of childhood and for the management of schools. It is a pleasure to acknowledge the valuable assistance that I have enjoyed in this work on the part of the Department of Education, and particularly of the Superintendent of Schools of Utuado, Mr. Blanco, and of all the teachers of that town.

The data thus obtained give also valuable information on the type of Porto Ricans and necessitated studies among the adults. Material for these has been obtained, particularly among the soldiers of the Porto Rican regiment, and the success of this work is entirely due to the liberal assistance of Major Basil H. Dutcher. It is not possible yet to speak of the results of this work with certainty, but it would seem that a remarkably strong environmental influence upon the racial type of man may be observed. If this should prove to be the case, we should have succeeded in establishing a fact of great scientific importance.

The collection of folklore in Porto Rico was entrusted to Dr. J. Alden Mason, who solved his task with great skill and success. He has accumulated many hundreds of folk tales, riddles, rhymes, ballads, songs, which will give us a clear insight into the traditional literature of the island. I think the material, when worked out and published, will have not only great value for the study of Romanoc philology and comparative literature, but will also furnish reading matter for the rural schools, attractive and interesting to the children, because based on their own historic environment. It should have an influence similar to that of the European fairy tales, collected a century ago, which have been a source of pleasure and instruction for millions.

The archæological work has been carried on by Dr. H. K. Haeberlin, Mr. Robert T. Aitken and Dr. J. Alden Mason. Dr. Haeberlin investi-

gated with great care one stone inclosure (*juego di bolas*) in the Jobo district and a cave near by. The latter contained some ceremonial objects and a small number of burials. In the cave were found large numbers of bones of an extinct rodent that may have been used for food.

Messrs. Mason and Aitken excavated a large cave in Caguana, Utuado, which proved to be the burial ground of an ancient community. Here also a large number of bones of extinct rodents were found. At the foot of the hill in which the cave is situated were found terraces and inclosures, evidence of the existence of an ancient village, to which undoubtedly the cave belonged.

After the cave had been cleared out completely, Messrs. Aitken and Mason took up a preliminary investigation of a village site at Capa, located by the writer, that seemed of particular interest. For the present half year the committee has contributed considerable funds for research at this site, which proves to be by far the most important of all archaeological localities so far investigated in Porto Rico. Dr. Mason has been carrying on work there throughout this half year, with the exception of a period of about four weeks. He closed his field work on the 15th of December, although not more than about one third of the whole site has been excavated. An accurate survey of the site is being made.

The locality seems to be so important that it ought to be preserved, and I trust that the Government of Porto Rico may find it possible to protect it temporarily by detailing a policeman to watch it, and permanently by acquiring the site as a national monument.

4. BOTANY

BY PROFESSOR N. L. BRITTON

Botanical exploration was continued at the end of 1914 by Professor N. Wille, of the University of Christiania, Norway, an expert in the study of fresh-water and aërial algæ, who was sent to Porto Rico under the auspices of the New York Botanical Garden. He made large collections of these minute or microscopic plants, which proved to be unexpectedly numerous and about which very little was previously known in the American tropics. His collections show that several hundred species inhabit Porto Rico, many of them entirely new to science, including several undescribed genera. Subsequent studies of the vast collections made by him, comprised in over 2,000 field numbers and including 10,000 specimens or more, will require much time and will be a noteworthy contribution to biology. Professor Wille was subsequently joined by his wife and they remained on the island until March, 1915.

In February, 1915, Dr. N. L. Britton, accompanied by Mrs. Britton, by Mr. John F. Cowell, Director of the Buffalo Botanical Garden, and by Mr. Stewardson Brown, Curator of Botany at the Academy of Natural Sciences of Philadelphia, came to Porto Rico, and the party made botanical studies and collections at several places on the northern coastal plain, in the western and central mountains, and at several points on the coast, by means of a sloop, from Mayaguez to Cabo Rojo Lighthouse and Ponce, including an examination of Cayo Muertos, the botany of which was previously unknown. Collections aggregating some 6,000 specimens were made, and the study of these is progressing. Special attention was paid to the few forested areas remaining.

Dr. Marshall Avery Howe, a Curator at the New York Botanical Garden, expert in marine algæ, spent about a month in June and July in continuing his previous studies and collections of these plants in the waters from Cabo Rojo Lighthouse to Ponce, also visiting Cayo Muertos, and obtained about 3,000 specimens.

Professor F. L. Stevens, formerly Dean of the College of Agriculture at Mayaguez, visited Porto Rico between June 9 and August 18, 1915, under the auspices of the University of Illinois and of the New York Botanical Garden, for the purpose of continuing his studies and collections of the parasitic fungi. During this period he visited nearly all parts of the island and collected many thousand specimens, the study of which will add greatly to our knowledge of these plants, many of which are destructive to vegetation.

Professor Bruce Fink has recently gone to Porto Rico for mycological and lichenological study, intending to remain there for several months, and has generously offered to contribute the results of his work to the Survey.

N. L. BRITTON,

Chairman.

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- 1887. Sir HENRY ENFIELD ROSCOE, London, England.¹
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